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The Canadian Entomologist

VOLUME XCI AUGUST 1959 NUMBER 8

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PUBLISHED MONTHLY

by the Entomological Society of Canada and the Entomological Society of Ontario with the assistance of Le Ministère de l'Agriculture de la Province de Québec.

AUTHORIZED AS SECOND CLASS MAIL BY POST OFFICE DEPARTMENT, OTTAWA, pp. 91

The Canadian Entomologist

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The Canadian Entomologist

Vol. XCI Ottawa, Canada, August 1959 No. 8

The Interaction of the Spruce Budworm, *Choristoneura fumiferana* (Clem.), and the Parasite *Apanteles fumiferanae* Vier.[1]

By C. A. Miller[2]

Introduction

In the late 1940's significant increases in the population of the spruce budworm, *Choristoneura fumiferana* (Clem.), occurred in northern New Brunswick and culminated in a severe outbreak of this major forest pest. The outbreak has been the subject of intensive investigations dealing with emergency chemical control operations (Webb, 1956) and with a long-term study of the population dynamics of the budworm. The latter program, called the Green River Project, is located on the Green River Watershed in northwestern New Brunswick. Its objectives, the co-operating agencies involved, the mortality factors being studied, and methodology have been discussed elsewhere by Morris *et al.* (1956), Morris (1951), Morris and Miller (1954), and Morris (1955).

One of the primary aims in the analysis of the data obtained on natural mortality factors in the Green River area is the development of a mathematical model of budworm survival, which, ideally, will contain a number of structural sub-models mimicking the effect of individual mortality factors on the budworm. This paper deals with the analysis of field data on the interaction of the parasite *Apanteles fumiferanae* and the budworm by means of a structural model. The model was developed and fully described by Watt (1959).

A. fumiferanae is treated here only as a mortality factor and not as a potential regulator of budworm density. Further, the data presented date from 1950 and the budworm was already increasing rapidly in the study area by that time. Results and conclusions are therefore based on outbreak conditions and may require some modification if applied to endemic populations. For example, limited data indicate that, whereas *A. fumiferanae* is a common parasite during an outbreak, it is relatively scarce during the endemic period. A major shift in the parasite complex of the budworm may occur between these two periods since the degree of attack by parasites such as *Horogenes cacoeciae* (Vier.) and *Exochus* sp. that are common during the endemic period is apparently inversely related to major changes in host density. No reference is made to the existing theories of host-parasite interaction since these have already been discussed by Watt (1959).

Description of Study Plots

All but one of the permanent study plots are situated on the Green River Watershed and adjacent parts of the Kedgwick and Iroquois Watersheds. The letters G, K, and I are used respectively to distinguish plots on the Watersheds as shown in Table I. Balsam fir (*Abies balsamea* (L.) Mill.) is the predominant species in the valleys and lower slopes, with white spruce (*Picea glauca* Voss) mixed with the fir in valleys, and white birch (*Betula papyrifera* Marsh.) mixed in varying proportions with the fir on all slopes. However, birch dieback killed most of the birch throughout the area before 1945. The softwood forest is typically mature, interspersed with middle-aged dense stands of balsam fir dating from the spruce budworm outbreak of 1912-1920. Table I lists the study plots

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TABLE I

Description of Study Plots, Including First-Instar Budworm Populations for the Period 1950–57

Plot	Age	Average tree diameter breast high	Total basal area per acre	Per cent of basal area fir and spruce	Number of larvae per 10 square feet of foliage							
					1950	1951	1952	1953	1954	1955	1956	1957
			(sq. ft.)									
G 2	90	6.9	87.7	88	26	16	58	295	52			
G 4	90 130[1]	8.0	94.6	95	343	169	155	472	117	40	340	16
G 5	40	3.7	130.1	96	18	5	32	130	6	34	54	
G 6	60	6.0	166.1	66					328	425	1324	s
G 8	90	9.0	109.4	90		282	511	481	70			
G 9	90	7.8	107.7	91		(2520)[2]	1980	s	258	1470	s	
G 11	40	3.5	164.5	95			(469)	362	29			
G 12	40	3.6	162.2	95			(803)	511	299	520	253	
K 1	90 130	6.8	107.3	90		(2472)	1058	685	185	420	696	43
K 1-S										(1024)	2254	182
K 2	40	3.0	78.8	95		(444)	1022	559	228	643	364	16
K 3	40	3.4	142.5	97				s	(391)	1780	s	
I 1	40	2.5	78.8	76					246	1826		
N 1	30	4.2	20.5	100							1238	486

[1]Two age classes.
s = sprayed with DDT.
[2]Data not used in analysis, since parasite density unknown in that year.

with age and stand density. Plot G2 is an example of a mature softwood stand while plot G5 is a typical balsam middle-aged stand. Two plots in Table I need further description. Plot K1-S refers not to an area, but to the scattered white spruce component on Plot K1. Balsam fir mortality has occurred on this plot and budworm populations are being followed separately on white spruce and the surviving fir. Plot N1 is a white spruce stand on Cape Breton Island, Nova Scotia, and is typical of areas where the budworm persists over a long period of time at a relatively high density (Morris, 1958).

Table I also shows the population density of first-instar larvae (egg counts less egg mortality) on the study plots for the period 1950-57. Data were obtained each year on some plots, whereas other plots were discontinued owing to cutting operations and aerial spraying, or new plots were established as the budworm spread from focal points into new areas. The counts show that on one group of plots (G2, G4, G5, G8) populations remained at a relatively low level while on a second group (especially G12, K1, K2) they were sufficiently high to cause 100 per cent current defoliation for successive years resulting, by 1958, in 78 per cent tree mortality on K1, 68 per cent on K2, and varying degrees of 'top-killing' on G12. These two groups of plots will be referred to as areas of intermediate infestation and severe infestation respectively.

Apanteles fumiferanae Vier.

A. fumiferanae is a small braconid parasite that attacks the spruce budworm throughout the range of this forest pest in Canada and the United States (Wilkes *et al.*, 1948), (Dowden *et al.*, 1948). It also attacks *Dioryctria abietella* (D. & S.) (Muesebeck *et al.*, 1951), and in the Green River area a few specimens have been reared from *Dioryctria reniculella* Grote. This latter species, like the budworm, overwinters as a small larva. Benjamin and Drooz (1954) record it as a parasite of the jack-pine budworm (*Choristoneura pinus* Free.) in Michigan. In general, however, *A. fumiferanae* may be considered a specific and univoltine parasite.

The life histories of the spruce budworm and *A. fumiferanae* in the Green River area and their synchronization are approximately as follows:

Time	*Host stage*	*Parasite stage*
Late July to early August	Egg	
Early August	First instar	Adult
Mid-August	Second instar	
Mid-August to mid-May	Second instar in hibernaculum	Egg
Early June	Third instar	First-instar larva
Mid-June	Fourth instar	Mature larva
Mid-June to early July	Fifth and Sixth instar	
Mid-July to late July	Pupa and adult	Cocoon

Brown (1946) states that "emergence of the adult parasite coincides with the hatching of budworm eggs". The adults probably feed on flowering plants and shrubs in the field since cage experiments indicate that individuals without food die shortly after emergence while those fed on an aqueous solution of honey have a mean longevity of 21 days for males and 36 days for females.

Flanders (1956) states that "the *Apanteles* egg is hydrophic and thus utilizes the embryonic membrane to obtain nourishment from the host's fluids. The

eggs are stored in an enlarged oviduct which is an adaptation permitting restraint in oviposition so essential to host selection".

McGugan (1955) cites data to show that the mature parasite larva emerges from the third-, fourth-, or fifth-instar host, with the majority emerging from the fourth instar. Emergence from the fourth-instar host is most common in the Green River area. Observations in rearing cages indicate that the mature larva migrates to a secluded site and spins a cocoon; in the field cocoons are found among needles and under bark scales. Approximately 10 to 12 days are spent in the cocoon stage.

The fecundity of *A. fumiferanae* was assessed in a series of oviposition experiments using a glass jar of one pint capacity with an open-weave cotton cover as a cage. One male and one female were placed in each cage with 150 to 450 budworm eggs, a number of balsam-fir shoots, and raisins soaked in a honey solution. The shoots provided hibernation sites for the emerging first-instar budworm larvae. Mating was observed and the female parasite was also observed attacking freely moving first-instar larvae, actively searching the shoots, and apparently attacking the first- and second-instar larvae in hibernacula.

When the female parasite died the host larvae on the balsam fir were placed in cold storage to overwinter (Miller, 1958); the larvae were forced from hibernation in the spring, and either dissected for parasite larvae or reared to obtain the parasite adults. Mortality in the rearing program was high owing to the difficulties in handling second-instar larvae. The results of 10 oviposition experiments were analysed on the basis of the number of parasitized second-instar hosts emerging from hibernacula in the spring. The data showed a mean parasite fecundity of 102 eggs, ranging from 38 to 192, assuming that the degree of attack was equal among dead and living hosts.

Table II shows the distribution of parasite larvae among attacked hosts in five oviposition experiments. Superparasitism occurred only in one experiment, indicating that the female shows a degree of discrimination even in a confined environment.

It is impossible to draw conclusions on the searching and oviposition behaviour of *A. fumiferanae* from field studies directed primarily toward population ecology of the host, but tentative conclusions may be drawn from data on host density and the degree of parasite attack. Table III shows rank-correlation coefficients between the degree of *A. fumiferanae* attack and second-

TABLE II

Summary of *A. fumiferanae* Oviposition Experiments

Experiment	Host population provided	Hosts examined for parasites	Frequency of parasites within hosts				
			0	1	2	3	4
1	244	80	56	24			
2	277	219	189	30			
3	217	60	33	27			
4	383	100	70	30			
5	285	190	77	105	5	2	1

TABLE III

Rank Correlation Coefficients between Degree of *A. fumiferanae* Attack and Host Density on Individual Trees

Plot	Year	No. of trees sampled	Host population range per 10 sq. ft.	tK[1]	P
G12	1956	5	92–227	.80	.04
K2	1956	5	101–473	.60	.12
I2	1956	5	147–260	.00	.60
K3	1956	5	382–869	−.40	.76
13-B	1956	10	206–437	−.42	.95

[1]Kendall's tau statistic.

instar host density on individual fir trees. On only one plot in five (G12) is there a significant correlation. However, it must be noted that only a small number of trees was sampled and also that some of the hosts were probably subject to inter-tree dispersal after attack (Miller, 1958). A similar study was carried out in three plots in 1958 where population densities ranged from one to 20 larvae per 10 square feet of foliage. Results were inconclusive owing to the small number of larvae collected per tree, but again did not suggest a relationship between degree of attack and host density.

Variation in the degree of attack at different heights within tree crowns was also investigated. Five trees were sampled and approximately 1,500 second-instar larvae were collected from hibernacula and separated into two groups on the basis of hibernation site within the crown. Dissections showed 19 per cent parasitism in the top half of the crown, but only seven per cent in the bottom half. This differential attack is not solely related to host density but may also include the effect of a physical factor, such as light intensity (Miller, 1958). Jaynes (1954) obtained similar results from intra-tree studies of parasitism caused by *A. fumiferanae* in Maine.

The effects of the food plant of the host on parasite behaviour have not been investigated thoroughly since budworm population studies have primarily centred on balsam fir, the favoured food plant and the predominant species on most plots. On Plot K1, however, budworm counts have been made on both balsam fir and white spruce. Table IV shows that in the declining years of an infestation, and after severe balsam fir mortality, budworm populations are higher and the degree of parasite attack is greater on white spruce than on the surviving balsam fir. The difference in attack is not only a function of the three-fold difference in host density but is probably also influenced by a preference for white spruce foliage over severely defoliated balsam fir suggested by olfactometer experiments with parasite females.

The low incidence of superparasitism in laboratory and field studies and the higher degree of attack in the upper crown levels suggest that searching by the individual female is not entirely random. Field data suggest that the parasite is guided by certain sensory mechanisms which cause it to: (a) discriminate between parasitized and non-parasitized hosts, (b) go to the upper levels of the crown, and (c) choose foliated spruce over heavily defoliated fir. The spatial relationship between the degree of attack and host density is not well defined except

TABLE IV

Comparison of Degree of *A. fumiferanae* Attack on Balsam fir and White Spruce, Plot K1, 1955-1957

Year	Tree species	Budworm population per 10 sq. ft.	Tree mortality[1]	Per cent parasitism
1955	Balsam fir (B)	420	15	10
	White spruce (S)	1024	0	20
1956	B	696	44	15
	S	2254	0	19
1957	B	43	70	19
	S	182	0	26

[1]Percentage based on basal area of balsam fir.

where more than one species of host food plant is considered and, in this instance, factors other than host density confound the relationship. A major difficulty arising from this type of parasite behaviour is the accurate assessment of the degree of parasite attack. Consequently, the estimate of per cent parasitism is based on the pooled samples of host larvae collected on a proportionate basis from four crown levels on each of 10 trees per plot.

Estimation of Parasite Density and Number of Hosts Attacked

Indices rather than absolute population data are used in estimating both parasite density and the number of hosts attacked. The reasons for using indices, and the underlying assumptions, are discussed in the following sub-sections.

Number of hosts attacked.—*A. fumiferanae* attacks either 'freely-moving' first-instar larvae or first- and second-instar larvae in hibernacula, although it is probable that the parasite attacks larvae in hibernacula more frequently. However, during the period from eclosion to formation of hibernacula the host population is subject to severe losses as the result of dispersal and other factors. A comparison of first- and second-instar populations shows reductions ranging from 50 to 80 per cent (Miller, 1958). Thus, the parasite attacks a portion of the population that is constantly changing in time and consequently difficult to measure in the field. Since no relationship exists between host density and first- to second-instar mortality, the data are treated as if *A. fumiferanae* attacked the first-instar population and this density is used in estimating the number of hosts attacked. (The first-instar population is obtained from egg counts less egg mortality.)

The number of hosts attacked is the product of the first-instar host density and the percentage of the hosts parasitized. This percentage is obtained from the dissection or rearing of third- and fourth-instar budworms collected during population sampling of four crown levels of each of 10 trees per plot (Morris, 1955). In the period 1949-1958 approximately 18,000 larvae were examined for the presence of *A. fumiferanae*.

Per cent parasitism based on third- and fourth-instar collections assumes that no differential mortality between parasitized and non-parasitized hosts occurs from the time of attack to the time of collection. Host mortality is high during

TABLE V

Comparison of Estimates of Per Cent Parasitism Based on Second and Third Instar Dissections

Plot	Instar	No. of Larvae dissected	*Apanteles* parasitism	P
G12	II	610	6.7	>.05
	III	147	11.6	
K2.....	II	620	10.2	>.70
	III	200	11.0	
K3.....	II	540	11.7	>.50
	III	200	13.0	
K2.....	II	170	12.4	>.50
	III	139	15.8	

this period as a result of fall and spring dispersal losses and a comparison of second- and third-instar larval dissections show that the assumption is correct. Although Table V shows that estimates of parasitism by *A. fumiferanae* are consistently higher for third-instar dissections than for second-instar dissections, the differences are not significant. However, should it prove that a significant differential mortality between parasitized and non-parasitized larvae does occur during the spring dispersal period, the model could easily be modified to include this effect.

The fact that *A. fumiferanae* attacks a greater proportion of hosts in the top half of the tree also creates difficulties in estimating mean per cent parasitism. This difference is diminished by dispersal of second-instar larvae in the spring but it is not entirely eliminated. Dissections of third-instar larvae from two crown levels (Table VI) also show a higher proportion of parasitized larvae in the top half of the crown. The budworm-sampling technique, however, provides an equal intensity of sampling from each of four crown levels (Morris, 1955) and the probability of obtaining a biased estimate of parasitism is slight when all the larvae in each tree sample are examined for parasites. Examination of all larvae in the tree sample is carried out at low to moderate population levels. The probability of bias could increase at high population levels when only a portion of

TABLE VI

Per Cent Parasitism Based on Third-Instar Collections from Two Crown levels

Year	Plot	Top		Bottom		P
		Total larvae examined	Per cent parasitism	Total larvae examined	Per cent parasitism	
1952	G8	240	18	256	11	<.05
1953	G8	90	19	146	7	<.01
1953	G4	71	32	100	22	>.10

the larvae in the sample are examined, but is, in effect, eliminated because the branch samples are pooled and thoroughly mixed during the collection period.

A further source of error in estimates of parasitism can occur when such estimates are obtained from both mass rearing and dissections. Dissections, as may be expected, give higher estimates of parasitism than rearings. This discrepancy arises partly from the difficulty in assessing the fate of all individuals that die in mass rearings, and partly from the fact that dissections may include species of *Apanteles* that cannot be separated in immature stages from *A. fumiferanae*. Small numbers of the following species have been reared from the spruce budworm but the larval forms have not been recognized in dissections.

A. petrovae Wly.
Apanteles sp. 51, near *tischeriae* Vier.
Apanteles sp. 24[3]
A. polychrosidis Vier.

Two of these species, *A. petrovae* Wly. and *A. polychrosidis* Vier., are recorded by Krombein (1958) as parasites of the budworm.

It may therefore be concluded that discrepancies can arise in estimating per cent parasitism depending on the host stage investigated and the technique used in detecting the parasite. But no systematic errors have been found of a magnitude to warrant corrections of per cent parasitism based on third- and fourth-instar dissections.

Adult parasite density.—The technique of caging foliage samples during the cocoon stage of *A. fumiferanae* and collecting the adults in emergence vials has been investigated as a means of assessing parasite density. The results were encouraging but insufficient data were obtained on the efficiency of the technique to permit firm conclusions. Therefore adult parasite density is calculated as the product of the host density at the time of initial parasite emergence (fourth-instar) and the percentage of the hosts containing parasites. The use of larval population trends in estimating this figure has been described (Miller, 1954). Thus, the potential number of hosts killed by the parasite is used as an index of the number of adult parasites emerging in that generation. Parasite mortality during the emergence period, the cocoon stage, and the adult stage is not known. Further, a parasite-population index and not a female-parasite index is used in the analysis since dissection of larvae prevents the collection of intensive data on sex ratios.

Analysis

The development of the mathematical model used in the following analysis is discussed in detail by Watt (1959). However, some equations are repeated here for ease of reference.

Definition of symbols.—

N_A = number of hosts attacked
N_0 = number of hosts vulnerable to attack
N_{0_p} = number of hosts in previous generation
P = number of parasites searching
A = coefficient of attack, or the number of hosts attacked per parasite and considered an instantaneous rate
K = the maximum number of attacks that can be made per parasite when the hosts are vulnerable

If all parasites can generate a total of PK attacks and $\delta N_A/\delta N_o$ diminishes gradually as N_A approaches this maximum, then,

[3]Species identification number.

$$\frac{\partial N_A}{\partial N_O} = PA(PK - N_A) \quad (1)$$

but, $A = aP^{-b}$ where a and b are positive constants. (2)

Substituting (2) in (1) gives

$$\frac{\partial N_A}{\partial N_O} = PaP^{-b}(PK - N_A) \quad (3)$$

integrating,

$$-\ln(PK - N_A) = -\ln PK + N_O PaP^{-b} \quad (4)$$

which gives $N_A = PK(1 - e^{-aN_O P^{1-b}})$ (5)

Equation (5) expresses the number of hosts attacked in terms of the number of parasites searching and host density. The symbol K refers to the maximum number of attacks made per parasite and in the following analysis it is shown that K = 70 where P, the number of parasites, includes both sexes. However, the biological meaning of K is more evident if considered in terms of a value for females. Thus a K value for females (sex ratio 1:1) would be roughly 70 x 2 = 140. The term aP^{-b} refers to the searching and attack efficiency of the parasite. The constant a is, in effect, a measure of the attack rate per parasite in the absence of competition, and b is, in effect, a measure of intra-species competition and consequent reduction in the attack rate when more than one parasite is searching the environment. The following analysis is an attempt to fit this model to 55 sets of field data and thereby test its basic premises. Each set of data contain values for N_o, P, and N_A and the data were obtained during the period 1950-58 on the plots listed in Table I. The analysis is discussed under a number of sub-sections for purposes of clarity.

Relationship of N_A to N_o.—The 55 sets of data were first ranked on the value of P, and then divided into three equal groups. Fig. 1 shows the relationship of

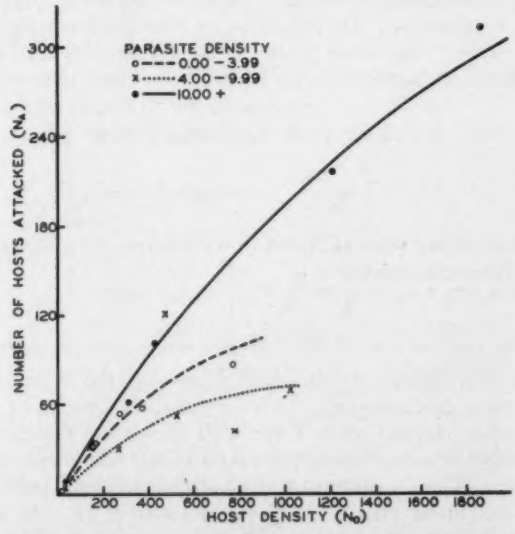

Fig. 1. The relationship of the number of hosts attacked to host density for three ranges of parasite density.

TABLE VII
The Relationship of the Number of Hosts Attacked per Parasite to Parasite Density

Plot	Year	Parasite density (P)	Host population per 10 sq. ft.	Host attacked per parasite (A)	
				(Observed)	(Calculated)[1]
G4	1956	1.78	340	32.1	38.2
"	1950	2.36	343	29.5	25.2
"	1952	8.35	155	4.00	3.88
"	1951	9.80	169	3.50	3.07
"	1954	15.10	117	1.40	1.47

[1]Where $A = 89\ P^{-1.4774}$

N_A to N_O for each group, that is, for three mean values of P. It indicates that N_A increases at a diminishing rate with an increasing N_o and reaches an asymptote and it is concluded that there is an upper limit to the number of attacks made per parasite. This is denoted by the symbol K in equation (5).

Relationship of A to P.—The concept that the average number of hosts discovered per female parasite decreases with an increase in parasite density has been proved by a number of investigators through laboratory experiments. Data in Table VII show that a similar relationship exists in field populations. Variate values for the number of hosts attacked per parasite (A) and parasite density (P) were subjectively chosen from one plot to minimize the range of host densities and the following equation was fitted to the data:

$$A = 89P^{-1.4774} \tag{6}$$

Table VII shows calculated values of A based on equation (6) consistent with observed values. Apparently the reduction in A with increasing P is a function of the competition for oviposition sites. It should be noted, however, that (6) is given only as an example and that these values are not incorporated into the model.

Estimation of K.—It follows from equation (4) that

$$\ln\left[\frac{PK}{PK - N_A}\right] = N_O P(aP^{-b}) \tag{7}$$

By holding P constant the term $aP^{-b}(=A)$ may be considered constant and a value for K obtained from the regression

$$\ln\left[\frac{PK}{PK - N_A}\right] = AN_O \tag{8}$$

where the value of K chosen is that which maximizes the correlation coefficient. Mean P values were calculated for each of the three groups of data that were ranked on the variate-value P, and Table VIII shows the correlation coefficients within each group for various assumed values of K. At mean parasite densities of 1.65 and 25.31 a K of 70 maximizes the correlation coefficients indicating that the maximum number of attacks made per parasite is 70. At a mean parasite density of 7.45, the data are less homogeneous, with a peak in the correlation coefficients occuring at K = 120. The results in Table VIII, however, do not

TABLE VIII

Correlation Coefficients for Assumed Values of K at Three Parasite Densities (See Text)

K values	Mean parasite density		
	1.65	7.45	25.31
40	r =	r =	r =
50		.542	.998
60	.964	.554	.998
70	.983[1]	.555	.999[1]
80	.981	.560	.998
90		.552	.997
100	.977	.566	
110		.566	
120		.589[1]	
130		.561	

[1]Peaks in correlation coefficients.

show that K is related to P in a density-dependent manner and it is assumed that 70 is the best estimate of the maximum number of attacks made per parasite.

Estimation of the constants a and b.—It follows from equation (4) that

$$\ln\left[\frac{PK}{PK - N_A}\right] = N_o P a P^{-b} \tag{9}$$

and

$$\frac{\ln\left[\frac{PK}{PK - N_A}\right]}{N_o P} = aP^{-b} \tag{10}$$

which becomes susceptible to linear regression in the form

$$\ln\left[\frac{\ln\left(\frac{PK}{PK - N_A}\right)}{N_o P}\right] = \ln a - b \ln P \tag{11}$$

With K = 70, the 55 sets of field data were analysed using equation (11). Data from one plot illustrate the procedure:
Where P = 0.82, N_o = 26.0, N_A = 3.89, K = 70
then

$$\frac{\ln\left[\frac{PK}{PK - N_A}\right]}{N_o P} \times 10^6 = 3302.1, \text{ and } \ln 3302.1 = 8.1017$$

and ln P = —0.1985. The constant 10^6 is used to give more easily manipulated values.

Fig. 2 shows the regression line for the 55 sets of data and this has a correlation coefficient of — .976 and gives the following values of *a* and *b*.

a = 0.00239
b = —2.0235

Estimation of the number of hosts attacked (N_{A_c}).—Equations (8) and (11) give the following values for *K*, *a*, and *b*.

K = 70
a = 0.00239
b = —2.0235

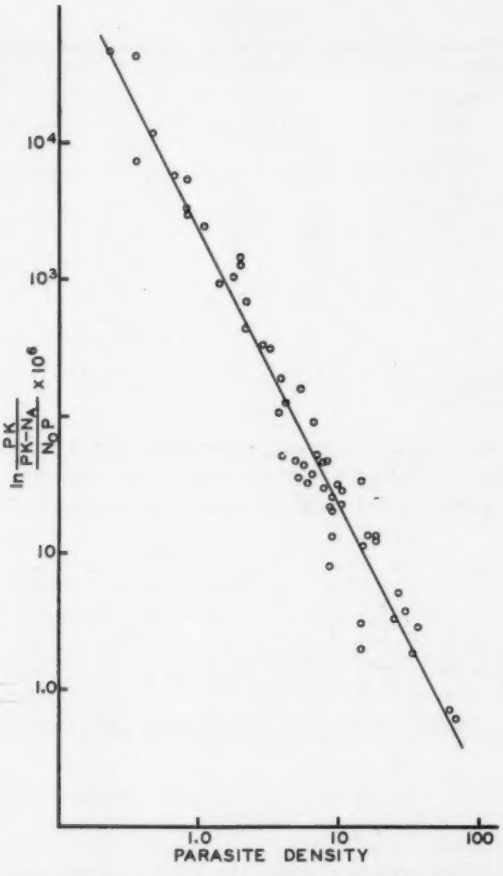

Fig. 2. A test of equation 10 to evaluate searching by *A. fumiferanae* for first-instar budworm. See text for definition of symbols.

and substituting these values in (5)

$$N_{A_c} = 70\ P(1 - e^{-.00239\ N_0 P^{-1.0235}}) \qquad (12)$$

The appropriate values of P and N_o were substituted in equation (12) to obtain N_{A_c} values. The example noted in the above sub-section is continued to illustrate procedure.

Where P = 0.82 and K = 70, PK = 57.40
Where b = − 2.0235, $P^{1-b} = P^{-1.0235} = 1.2252$
Where N_O = 26 and a = .00239, $aN_O = .621$
Then $aN_O P^{-b} = .07608$
and $1 - e^{aN_O P^{-b}} = .0732$
and $N_{A_c} = 57.40 \times .0732 = 4.20$ as compared with the N_A observed of 3.89

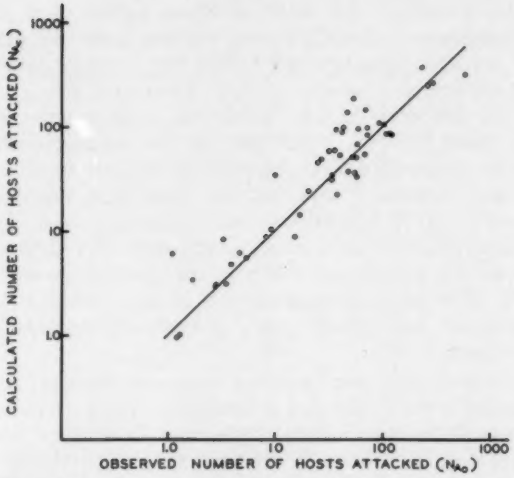

Fig. 3. The relationship of the calculated number of hosts attacked to the observed number of hosts attacked. Calculated data from equation 12 in text.

Fig. 3 shows the calculated values of N_A obtained from (12) plotted over observed values. It can be seen from this graph that N_{A_c} is generally underestimated or that the trend in the data is below the line of best fit, but parallel with it, and further, that a number of points are widely scattered from the line. Consequently, various attempts were made to improve the N_{A_c} values.

The relationship of N_{A_c} to other factors.—If N_{A_c} is related to any other factor, then a may be expressed as a function of that factor. Thus,

$$a = f(x) \tag{13}$$

Substituting (13) in (5) gives

$$\frac{\ln\left[\dfrac{PK}{PK - N_A}\right]}{N_O P^{1-b}} = f(x) \tag{14}$$

The following factors were examined using this relationship (14):

1. Host density
2. Host density in the previous generation
3. Host survival in the previous generation: (a) first to fourth instar
   (b) fourth to sixth instar
4. Parasite density
5. Number of rainy days: July 26 to August 20
6. Mean daily maximum temperature: July 26 to August 20
7. Stand factors: (a) degree of defoliation of current year's growth
   (b) yearly cumulative defoliation
   (c) number of trees per acre
   (d) average D.B.H.

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The analyses indicated that none of these factors was related to N_{A_c}. However, it was apparent from Fig. 3 that the points widely scattered from the line of best fit denoted plots situated within the severely infested area of the Watershed and applied to a period of time when host density was sufficiently high to cause 100 per cent current defoliation and, in most instances, severe thinning of the older foliage. Therefore, on the assumption that some event or series of events occurred during the peak of the infestation to upset the expected relationship between P and N_A, the data were split into two groups. One group consisted of 42 sets of data and included plots in the area of intermediate infestation and those plots in the severe infestation during the time when current defoliation did not exceed 100 per cent, that is, towards the end of the outbreak period. The other group of 13 sets of data included those plots where complete stripping of the current year's growth occurred for three or more successive generations.

The two groups of data were analysed separately in order to obtain separate parameter values for *a* and *b* and also to determine if any factor could be related on biological grounds to the observed difference in numbers attacked in intermediate and severe infestations. These analyses followed the same sequence outlined above and the methods will therefore be discussed only briefly.

Plots with less than 100 per cent current defoliation.—The 42 sets of data were re-analysed and with K = 70, the transformation (11) gave a correlation coefficient of -.991 and the following values for *a* and *b*:

$$a = .00277$$
$$b = -1.9685$$

Thus, the coefficient of attack

$$A = .00277\ P^{-1.9685} \qquad (15)$$

A comparison of (15) with the parameter values for A ($= .00239\ P^{-2.0285}$) in equation (12) shows that the former gives an increased number of hosts attacked per parasite but shows little difference in the rate of change in attack with increasing parasite density. This is to be expected since equation (12) underestimates N_A over a wide range of parasite densities. It is therefore assumed, on the basis of this analysis of 42 sets of data, that equation (15) is the best estimate of the attack coefficient of *A. fumiferanae*.

Plots with successive years of 100 per cent current defoliation.—The 13 sets of data in this group of plots hardly provided a sufficient number of variates from which to estimate a new K value. Table IX shows that when all 13 sets of data were considered the regression coefficients based on equation (8) are bimodal. (The variability in the data is also shown in Table VIII in the initial analysis of K at intermediate parasite densities.) By plotting $\ln(PK-N_A)$ over N_o the data were observed to fall into two distinct groups and values of 70 and 90 were calculated respectively for each group (Table IX). However, since the value of 90 could not be related to any one year, plot, or to parasite density, it was assumed that a K of 70 was still the best estimate of the maximum number of attacks per parasite.

The difference between the observed number of hosts attacked for the 13 sets of data and the calculated values from equation (12) was then examined to see if this difference was related to such factors as host density, parasite density or various stand factors. A relationship was found between the ratio N_{A_o}/N_{A_c} to host density in the previous generation, N_{o_p}. Since parasite density is related to N_{o_p} it was assumed that some mortality factor becomes increasingly effective

TABLE IX

Correlation Coefficients for Assumed Values of K. Data from 13 Plots in Severe Infestation (See Text).

K values	Mean parasite density		
	All 13 plots 8.22	Group 1 7.50	Group 2 9.06
10	r = .893[1]	r =	r =
20	.840	.926	.464
30	.830		
40	.827	.932	
60			.486
70		.933	.568[1]
80		.935	.517
90		.938[1]	
100		.935	.504
120	.823		
130	.827[1]	.930	
140	.799		

[1]Peaks in correlation coefficients.

at high host densities to reduce the parasite population. Thus P_p, the measured index of parasite density is reduced to P_s. Watt (1959) shows that if this assumption is correct then

$$\frac{dP_s}{dN_{Op}} = -cP_s \tag{16}$$

and

$$P_s = P_p e^{-cN_{Op}} \tag{17}$$

The constant c may be obtained graphically or by regression analysis from the following equation (Watt, 1959, equation 26):

$$\frac{N_{A_o}}{N_{A_c}} = e^{-cN_{Op}} \tag{18}$$

The graphical method was used to find c by plotting the ratio N_{A_o}/N_{A_c} over N_{o_p} on semi-log paper and using that part of the line prior to the curvature caused by the exponential $\exp(-cN_{o_p})$. The following equation was fitted to the line:

$$\frac{N_{A_o}}{N_{A_c}} = e^{-.0006\,N_{Op}} \tag{19}$$

Substituting in (17) gives

$$P_s = P_p e^{-.0006\,N_{Op}} \tag{20}$$

Parameter Values in the Final Equation.—The analysis of the data in two groups provided new parameter values for the coefficient of attack and also showed that parasite populations are reduced by some mortality factor related to host density in the previous generation. These results are combined to give the final equation for estimating the number of hosts attacked by *A. fumiferanae*.

$$N_A = 70\,P_p e^{-.0006\,N_{Op}}(1 - e^{-.00277\,N_O P_s^{-.9885}}) \tag{21}$$

Equation (21) was used to calculate the number of hosts attacked for 50 sets of data and Fig. 4 shows the relationship of calculated to observed values.

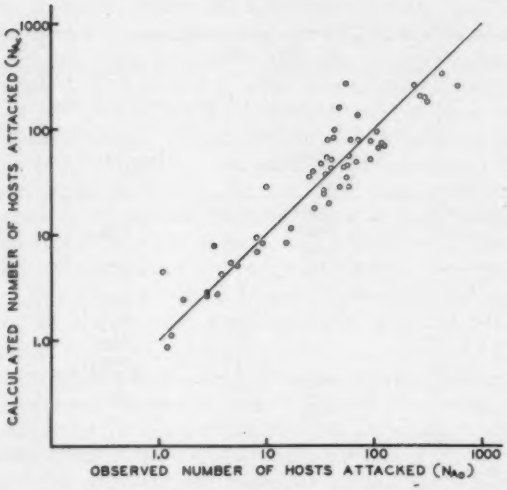

Fig. 4. The relationship of the calculated number of hosts attacked to the observed number of host attacked. Calculated data from equation 21 in text.

(The number of variates was reduced from 55 to 50 because N_{o_p} values were not known for all plots and years.) The correlation coefficient of this regression line is 0.843 indicating that the model explains 71 per cent of the variation in the number of hosts attacked. A comparison with the regression line in Fig. 3 ($r = .751$ for the same 50 sets of data as in Fig. 4) shows the improved fit resulting from changes in the attack coefficient and the inclusion of a parasite mortality factor.

Discussion

The spruce-budworm population data presented herein represent two rather distinct trends in the population behaviour of the spruce budworm in the Green River area in the period 1949 to 1958. Extensive defoliation surveys and limited sampling data show that a gradual increase in numbers occurred from 1945 to 1948. Then, over a large part of the area, populations increased rapidly over the next three years to a level where repeated stripping of the current year's foliage occurred. This resulted in the initial phase of tree mortality in 1954 and approximately 78 per cent mortality of balsam fir, four inches D.B.H. and over, by 1958 in areas of mature balsam fir reserved from aerial spraying. Fig. 5A, which shows yearly counts of first-instar budworm, illustrates this population behaviour. Fig. 5B illustrates the contrasting behaviour on the remaining area which was also reserved from aerial spraying but largely isolated by clear-cutting operations before 1950.

Fig. 5 also shows the contrasting trends in the population of the parasite *A. fumiferanae* in these two areas, particularly in the period 1952 to 1955 in the area of severe infestation (Fig. 5A). Evidence based on small random collections before 1949 in the Green River area, when host populations ranged from 0.05 to 0.10 larvae per 10 square feet of foliage, suggests that less than five per cent of the budworm larvae were attacked by this species. In the area of severe infestation per cent parasitism increased slowly to approximately 10 per cent in 1955, then rapidly to approximately 20 per cent in 1957. In the intermediate in-

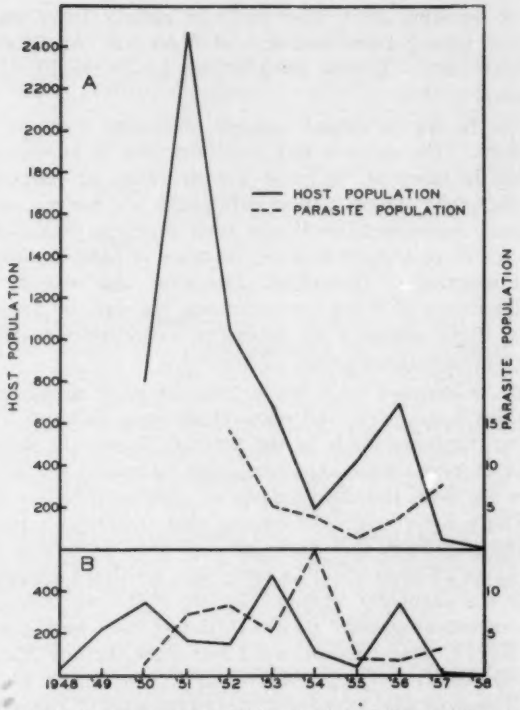

Fig. 5. First-instar budworm counts and the density of the parasite, *A. fumiferanae*, for the period 1948-58. The graph illustrates population trends of host and parasite in a severe infestation (A) and in an intermediate infestation (B). (Not to be confused with Fig. 3, Morris *et al.* (1956) where host density is based on a different stage and time scale.)

festation a sharp increase in parasitism to approximately 20 per cent occurred as early as 1950 and parasitism has fluctuated about this level during the outbreak.

The analysis of field data shows that a general mathematical model (Watt, 1959) will mimic and thereby evaluate the interaction of the spruce budworm and the parasite *A. fumiferanae* in these contrasting population trends with notable success. It also shows that certain discrepancies still exist between expected and observed values. The number of hosts attacked can be predicted with accuracy on plots where the population density remained at a relatively low level. But the model does not accurately evaluate the expected trend in parasite attack on plots and in years when food shortages occurred as a result of complete stripping of the current foliage. It overestimates the number of hosts attacked and this leads to the conclusion that, during the peak of a severe infestation, some factor or factors causes changes in either the number, physiological characteristics, or behaviour of the parasite that are not accounted for in the model. It is the aim of this discussion to enumerate some of the possible factors involved and their potential mode of action, and thereby to point out profitable areas of further research on host-parasite interaction.

Fecundity.—The effect of host starvation on the size of the issuing parasite, and more particularly on the fecundity of the parasite, is difficult to determine since fecundity is probably a function of both adult size and food intake. Linear

measurements of cocoons show that parasites issuing from starved hosts are smaller than those issuing from non-starved hosts but the effect on fecundity has not been determined. It may be surmised, however, that size is related to vigour and survival.

In the model, K, the maximum number of attacks made per parasite, is an index of fecundity. The analysis did not show that K is related to P, and in fact, a calculated K value of 70 fitted a wide range of parasite density, particularly for those plots where current defoliation did not exceed 100 per cent. The data did show inconsistencies where food shortage occurred, but failed to show a decrease in K, or suggest that the decrease in parasite efficiency in severe infestations is a function of fecundity. However, the estimate of K at intermediate and high values of P are uncertain and the data in Tables VIII and IX (bimodality and slight evidence of maximum correlation coefficients) suggest the necessity of further investigation.

Food supply.—Clausen (1940) states that the great majority of Braconidae feed principally on honey dew and plant exudations, although females of some species subsist on the body fluids of the attacked hosts. In instances where *A. fumiferanae* was observed attacking first-instar budworm the female apparently did not feed on the host, but did feed on an aqueous solution of honey placed in the cage. There is no reason to suspect that food was a factor limiting *A. fumiferanae* attack during the outbreak on any particular plot. Ground-vegetation studies on all plots based on systematic quadrat sampling show a marked similarity in the recurrent groups (Fager, 1957) of flowering plants and shrubs. These recurrent groups always include *Oxalis montana* Far., *Clintonia borealis* (Ait.) Raf., *Cornus canadensis* L., and often include *Maianthemum canadense* Desf. and *Rubus strigosus* Michx. The one major change in ground vegetation has followed the advent of tree mortality in the severe infestation area. Here, increases in the shrub layer (*Rubus strigosus*) has reduced the abundance of some flowering plants but these changes, occurring late in the outbreak, cannot be related to the observed limitations in *A. fumiferanae* attack.

Parasite mortality.—Parasite density is a function of host density in the previous generation, N_{o_p}, and the analysis of the relationship of N_{A_O}/N_{A_C} to N_{o_p} (equation 19) shows that a factor or combination of factors causes a reduction in the survival of parasites particularly when host density in the previous generation is high. Thus, P_p, the measured index of parasite density, is reduced to P_s, the actual number of parasites searching. Among the factors that could contribute to this reduction are: mortality of parasitized hosts, and changes in the sex ratio, since both may be related to N_{o_p}.

Mortality of parasitized larvae.—The index of parasite density P is based on the host density at the initial period of parasite emergence and does not include mortality of parasitized larvae during the two-week emergence period in the latter part of June. In a severe infestation food shortage occurs during this period, and larvae tend to drop from the upper to the lower portions of the crown and to understory trees in search of a new food supply. Thus, a greater mortality may occur, particularly among the less active parasitized hosts, as a result of this intra- and inter-tree movement in a severe infestation, than takes place in an intermediate infestation where food shortage is not a critical factor.

Sex ratio.—Flander (1956) in a discussion on the sex ratio in parasitic Hymenoptera states that "In species with small spermathecal glands such as the bracon type, host density influences the sex ratio of the parasite through its effects on

TABLE X

Sex Ratio[1] of *A. fumiferanae*

Year:	1951	1953	1954	1957	1957[2]	1958
Adults examined	90	32	135	69	26	45
Sex ratio (as per cent females)	46	53	46	59	59	58

[1]Data do not apply to one particular plot.
[2]Field-Collected cocoons.

the rate of oviposition. Activation of the sperm may not keep pace with egg deposition and this results in a preponderance of male progeny". The concept that sex ratio may change in time and place is recognized although only limited data were obtained on this factor in any one year (Table X). A preponderance of males could have occurred at very high host densities on the basis of the theory cited by Flanders. This in effect would act as a mortality factor reducing the parasite population since the population index, P, is based on the total number of individuals and not on the number of females.

However, it must be concluded that parasite mortality does not entirely explain the less effective action of *A. fumiferanae* in severe infestations, although it does apparently increase with increasing host density and a number of factors either singly or in combination could contribute to it.

Cocoon mortality including hyper-parasitism.—No adequate estimates of cocoon mortality resulting from predation and hyper-parasitism were obtained during the study, although the hyper-parasite *Gelis* sp. was reared from random cocoon collections.

Limitations in assessing parasite oviposition behaviour.—It has been assumed in equation (21) that the oviposition behaviour of *A. fumiferanae* is relatively constant throughout a host density range from five to 2,000 per 10 square feet of foliage. This assumption may be questioned since host density can have a modifying effect on the oviposition behaviour of the parasite as shown by Burnett (1958) and Wylie (1958). Oviposition behaviour may be such that, at very high or very low host densities, parasite progeny may tend to be found in 'pockets' within the population. This type of behaviour would be difficult to demonstrate by field sampling techniques where the degree of parasite attack is based on the mean of pooled samples. Thus, the limitations set by sampling methods in accurately assessing parasite attack cannot be ignored, particularly at extreme ranges of host density where the sample is either a very small proportion of the population available to attack, or time and effort limit the number of hosts that can be collected for examination.

Forest composition.—No relationship was found between variations in *A. fumiferanae* attack and forest composition. Table I shows that the study plots are relatively homogeneous except for differences in density associated with age, and the effect that density has on the abundance of ground vegetation. Thus, variations in composition are mainly limited to degree and not to major differences in tree species and ground vegetation complex.

Climate.—A number of weather factors, including mean maximum temperature, hours of rainfall, and amount of cloud, were tested against variation in *A. fumiferanae* attack and showed a surprising lack of relationship. However, the

effect of weather on this parasite may be partly obscured by the length of the attack period since cage experiments indicate a maximum longevity of 36 days.

Conclusions

The analysis of field data on the density of the parasite, *A. fumiferanae*, the density of the host, *C. fumiferana*, and the number of hosts attacked shows that a mathematical model will mimic this host-parasite interaction to the extent that 71 per cent of the variation in the number of hosts attacked is explained by the model. The residual variation emphasizes the need for further research along two general lines: (a) field investigations on methods of assessing adult parasite density, and (b) controlled experiments on parasite behaviour and reproduction to obtain a better understanding of the coefficients contained in the model and of the extent these coefficients are related to the physiology, morphology, or behaviour of the parasite. This should indicate environmental factors that affect parasite efficiency and contribute to our knowledge of the possibility of manipulating the environment through silvicultural methods to improve natural control of the budworm.

Acknowledgments

I wish to acknowledge the valuable assistance of Dr. K. E. F. Watt in the analysis of the data, and the constructive criticism given by Dr. R. F. Morris and Mr. D. G. Mott during the preparation of the manuscript.

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(Received March 25, 1959)

Damage to Cabbage by the Clover Cutworm, *Scotogramma trifolii* (Rott.) (Lepidoptera : Phalaenidae)[1]

By L. M. Cass[2]

The clover cutworm, *Scotogramma trifolii* (Rott.), has been recorded from a wide variety of host plants, but there are few records in the literature associating it with cole crops. Riley (1893) recorded it from cabbage in Maryland. Gibson (1915) recorded it from turnip and cabbage in Canada. Forbes (1954) and Frost (1955) listed cabbage as a host plant in New York and Pennsylvania, respectively. In 10 years' studies on caterpillars on cabbage in the Ottawa Valley, 1949 to 1958, numbers of the clover cutworm on cabbage were almost always negligible. However, in the early summer of 1956 it occurred throughout the area in significant numbers, and in a study field of early cabbage at Merivale, Ontario, caused sufficient damage to affect the market value of the crop.

The feeding injury might easily be mistaken for that of the imported cabbageworm, *Pieris rapae* (L.), except that it is more confined to the developing head, which frequently becomes malformed. On June 22, at Merivale, one larva of the clover cutworm was found per plant; this was more than for the imported cabbageworm, the diamondback moth, *Plutella maculipennis* (Curt.), or the cabbage looper, *Trichoplusia ni* (Hbn.), which commonly attack cole crops in the Ottawa area. This appears to be the first record of the clover cutworm's causing damage of economic importance to cabbage.

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(Received March 17, 1959)

Parasites of the European Pine Shoot Moth, *Rhyacionia buoliana* (Schiff.), in Ontario[1]

By W. Y. Watson[2] and A. P. Arthur[3]

The European pine shoot moth, *Rhyacionia buoliana* (Schiff.), was introduced accidentally into Ontario about 1925, and has since spread throughout the southwestern part of the province south of a line from the south shores of Georgian Bay on the west to Brockville on the east (Fig. 1). Damage to the host is done by the larvae, the feeding of which results in the deformation of the branches and main stems, reducing the potential value of the trees as timber and, in heavy infestations, making young trees unsuitable for the Christmas tree trade. Several species of exotic and native pines are attacked; red pine, *Pinus resinosa* Ait., Scots pine, *P. sylvestris* L., and Mugho pine, *P. mugho* Turra, being the most susceptible. Because of the extensive planting of Scots and red pine in southern Ontario, especially during the last 25 years, the increasing numbers of European pine shoot moth in this area present a problem of great importance. Contributing to an understanding of this important pest, this paper presents a detailed review of the parasites obtained in Ontario since 1954, with some notes on earlier surveys.

Early records of parasites of the shoot moth in Ontario are given by de Gryse (Ann. Rept., Forest Insect Laboratory, Cedar Bay, Ontario, Can. Dept. Agr., 1932 and 1933, unpublished) and by Sheppard (1933). In 1951 a survey of the shoot moth was undertaken by the Belleville laboratory in the Brighton area (Northumberland County) and the following parasites were obtained: *Euderus subopacus* (Gah.), *Alegina* sp., *Horogenes* sp., and *Phaeogenes* sp. nr. *epinotiae* Cush. This survey was continued in 1952, yielding these additional species: *Orgilus obscurator* (Nees), *Calliephialtes comstockii* (Cress.), *Pimpla turionellae* (L.), *Hyssopus thymus* Grlt., *Itoplectis conquisitor* (Say), *Scambus* sp., *Eurytoma* sp., and *Habrocytus* sp. Of these *P. turionellae* and *O. obscurator* are introduced parasites, the former having been released in the area two weeks before the survey collection was made. The remaining parasites, which are indigenous, were also obtained from a pupal collection made at Wendover (Lambton County).

In 1953 parasite survey studies at the Belleville laboratory were extended to include Kingsville, Niagara Falls, Brock's Monument, Vineland, Hamilton, and Picton, as well as Brighton. The following parasites, the first three of which are introduced, were obtained: *Orgilus obscurator* (Nees), *Temelucha interruptor* (Grav.), *Tetrastichus turionum* (Htg.), *Calliephialtes comstockii* (Cress.), *Campoplex* sp., *Eurytoma* sp. prob. *pini* Bugbee, *Habrocytus* sp., *Hyssopus thymus* Grlt., *Itoplectis conquisitor* (Say), *Itoplectis* sp., and *Scambus hispae* Harr.

Also in 1953 Kirby (Interim Rept. 1954-4, Forest Insect Lab., Sault Ste Marie, Ontario, October, 1954, unpublished), working in the counties of Simcoe, Ontario, and Dufferin, obtained the following eight species of indigenous parasites: *Calliephialtes comstockii* (Cress.), *Eupelmella vesicularis* (Retz.), *Calliephialtes nubilipennis* (Vier.), *Eurytoma* sp. prob. *pini* Bugbee, *Scambus hispae* (Harr.), *Hyssopus thymus* Grlt., and *Itoplectis conquisitor* (Say).

In 1954 a comprehensive co-operative program was undertaken by the Forest Insect Laboratory, Sault Ste. Marie, and the Entomology Laboratory,

[1]Contribution No. 518, Forest Biology Division, and No. 3940, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.
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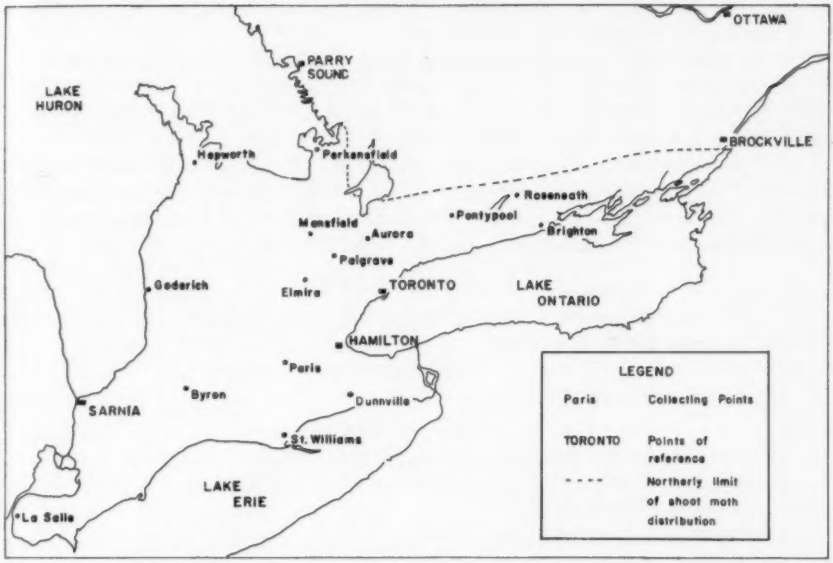

Fig. 1. Map of southern Ontario showing collection points of the European pine shoot moth and northern boundary of continuous distribution.

Belleville, Ontario, to survey the insect parasites of the European pine shoot moth throughout its range in Ontario. The Entomology Laboratory assumed responsibility for the survey in the Brighton area and the Forest Insect Laboratory, through the Forest Insect Survey, assumed responsibility for the survey elsewhere. Fifteen areas were examined between 1954 and 1956.

One species of dipterous and 22 species of hymenopterous parasites were obtained from the shoot moth during this survey.

Methods

Collections of 200 infested shoots were made at each of four stages (mid-larval, late larval, early pupal, early larval) of the insect's development from each area surveyed by Forest Insect Survey personnel. The collections were shipped immediately to the laboratory, where the host insects or parasitized host bodies were removed for individual rearing. The number of host insects taken from each collection of infested shoots averaged less than 200. Living larvae were placed on healthy red pine shoots in tall glass jars; pupae were reared in similar jars or in large vials. The larvae and pupae were allowed to develop with a minimum of disturbance. Emergent moths were discarded and parasite adults were killed and mounted.

During 1954 and 1955 the fourth collection, of early-instar larvae, was reared in the same manner, as the other collections, but considerable difficulty was experienced in inducing the young larvae to establish on new buds. Therefore, in 1956, the infested shoots were left undisturbed; four or five shoots were placed in each jar and the parasites allowed to emerge. These collections were retained until mid-September, when each shoot was dissected to disclose parasites that had developed but, for various reasons, had not emerged. Although this

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method did not give exact quantitative information, more parasites were obtained from the fourth collection.

Four collections, synchronized with those described above and each averaging about 300 host larvae, were made yearly at Brighton and reared at the Belleville laboratory. The insects were reared individually in glass shell vials (15 x 50 mm.) stoppered with copper screen plugs.

All parasites obtained at the Sault Ste. Marie laboratory were submitted to the Insect Systematics and Biological Control Unit, Ottawa, for identification. Similarly, all rare parasites and representative series of the commoner parasites were submitted to the same unit from the Belleville laboratory.

Parasites Obtained

The following parasites were reared from the European pine shoot moth during the years 1954-56 inclusive:

DIPTERA

Chloropidae: *Oscinella conicola* (Gr.).

HYMENOPTERA

Braconidae: *Bracon gelechiae* Ashm., *Orgilus obscurator* (Nees).

Eulophidae: *Elachertus* sp., nr. *pini* Gahan, *Elachertus* sp. nr. *proteoteratis* How., *Hyssopus thymus* Grlt.

Eurytomidae: *Eurytoma pini* Bugbee.

Eupelmidae: *Eupelmella vesicularis* (Retz.).

Ichneumonidae: *Atrometrus clavipes* (Davis), *Calliephialtes comstockii* (Cress.), *Campoplex* sp., *Gelis* sp., *Idemum* sp., *Itoplectis conquisitor* (Say), *I. evetriae* Vier., *Phaeogenes* sp. nr. *hebrus* (Cress.), *Pimpla aequalis* Prov., *P. turionellae* (L.), *Scambus hispae* complex, *Temelucha* sp., *T. minor* (Cush.).

Pteromalidae: *Habrocytus* sp., Pteromalini.

Notes on Parasites

The following information was obtained mainly from the present survey. Additional information on Ontario records was secured from the following sources; Canadian National Collection of Insects (CNC); Entomology Laboratory, Belleville (EL); Forest Insect Laboratory, Sault Ste. Marie (FIL); or literature. Information on the occurrence of these parasites outside of Ontario may be found in Thorpe (1930), Thompson (1943-55), and Muesebeck *et al.* (1951).

DIPTERA

Chloropidae

Oscinella conicola (Gr.)—A single specimen, tentatively identified as this species, was obtained from the mid-larval collection made at Perkinsfield, and emerged on June 1, 1956. This was the only dipterous parasite obtained from the collections, and its role as a parasite is questionable. The species is known to feed in red pine cones (CNC).

HYMENOPTERA

Braconidae

Bracon gelechiae Ashm.—A single specimen was obtained from the second collection made at Roseneath, and emerged on June 9, 1955. This species has also been obtained in Ontario from *Exoteleia dodecella* L. (CNC), *Phigalia titea* Cram. (CNC), and *Rhyacionia frustrana* (Comst.) (Cushman, 1927).

Orgilus obscurator (Nees).—This was the only species of introduced parasite commonly recovered. It was found in collections made at Dunnville, Byron, La Salle, St. Williams, Hepworth, Paris, Pontypool, and Brighton. The largest

consistent recovery was from Dunnville, where this species accounted for 87 per cent of the total parasitism. It was responsible for more than 50 per cent of the parasitism at Brighton in 1954, when 70 adults emerged, but was not recorded from this area in 1955, and only five specimens were obtained in 1956. Only three specimens were obtained from St. Williams and Paris in 1954-55 but there was a marked increase in 1956, when 23 specimens were taken from St. Williams and 72 from Paris. Although scattered single specimens have been recovered from many areas, this parasite is established mainly in the Niagara Peninsula, where repeated releases have been made since 1928 (Coppel and Arthur, 1954).

O. obscurator is an internal larval parasite, the development of which is occasionally delayed so that emergence takes place from the host pupa (Thorpe, 1930). The females oviposit in the early-instar host larvae during July and August, and the parasites overwinter as early-instar larvae within the hibernating host. Parasite development is resumed in the spring, the adults emerging between mid-June and mid-August. Three cases were recorded where two individuals emerged from single hosts.

Eulophidae

Elachertus sp. nr. *pini* Gahan—Two specimens of this unidentified species were obtained from the second collection at Elmira in 1955. Adults emerged on June 7.

Elachertus sp. nr. *proteoteratis* How.—One specimen of this unidentified species emerged on April 25, 1955, from the first collection made at Brighton. In addition three individuals were found overwintering as pupae inside a red pine shoot infested with *R. buoliana*. This species is a gregarious larval parasite.

Hyssopus thymus Grlt.—This species is a gregarious, external larval parasite and was obtained from all collection areas. It probably attacks all larval stages as it emerged from all four host collections. Adults emerged from late May until the end of July.

The females of this species enter the host tunnels, paralyse the larvae, and deposit from one to several eggs on or near the host. The winter is passed in the pupal stage within the tunnel made by the overwintering shoot moth larva. There are at least two generations and a partial third generation each year.

Eurytomidae

Eurytoma pini Bugbee—This species occurred sporadically in all areas. It was the most common parasite obtained from the second and third collections but was not obtained from the first collections. The species is a solitary, larval parasite, and is probably a secondary parasite as it will not oviposit on active shoot moth larvae in the laboratory. Adult emergence was from early June until late July.

Eupelmidae

Eupelmella vesicularis (Retz.)—One specimen was obtained from the third collection made at Brighton, the adult emerging on July 11, 1955. This species has also been taken in Ontario from *Coleophora* sp. (CNC), *Neodiprion abietis* (Harr.) (FIL), *N. lecontei* (Fitch) (FIL), *Rogas* sp. (EL), *Malacosoma disstria* Hbn. (EL), *M. pluviale* (Dyar) (EL), *Ceutorhynchus assimilis* (Payk.) (EL), and *Hylemya* sp. (EL).

Ichneumonidae

Atrometus clavipes (Davis)—One specimen emerged on July 10, 1954, from the third collection made at Brighton. This species is also recorded from *Ancylis comptana* Froh. in Ontario (CNC).

Calliephialtes comstockii (Cress.)—This large species was obtained from widely separated areas. It is a solitary, external, larval parasite, and was taken from the first three collections, but was most frequent in the third. *C. comstockii* overwinters on some host other than shoot moth, the adults emerging during May to attack the mid- and late-instar shoot moth larvae. Adults emerged from the shoot moth collections from late May until late July.

Campoplex sp.—Five specimens were obtained from the third collection made at Hepworth, the adults emerging from July 15 to July 20, 1954.

Gelis sp.—One specimen was obtained from the second collection made at St. Williams in 1955. The exact date of emergence is not known. Some members of the genus are secondary parasites.

Idemum sp.—Two specimens were obtained from the first collections made at the widely separated areas of Hepworth and Pontypool in 1954. The Pontypool specimen emerged along with a specimen of *Orgilus obscurator* from a single host. Adults emerged on July 3 and July 10.

Itoplectis conquisitor (Say)—This was a common species in the third collection made at Brighton in the years 1954-56, but was not found in the remainder of southern Ontario except at La Salle during 1954 and 1955. In 1956, however, it was obtained in both the second and third collections at Byron, Elmira, Goderich, Hepworth, and Paris. The species is a solitary, internal, pupal parasite which has been recorded from many lepidopterous hosts (Muesebeck *et al.*, 1951). *I. conquisitor* overwinters in some host other than *R. buoliana* and the adult parasites attack shoot moth pupae during late May and June. All but one of the adults emerged from the shoot moth from mid-June to mid-July; one adult emerged on August 8.

Itoplectis evetriae Vier.—Two specimens were found in the third collections made at Elmira and Roseneath in 1956. Adults emerged on July 18 from the Roseneath collection and July 23 from the Elmira collection.

Phaeogenes sp. nr. *hebrus* (Cress.)—One specimen of this unrecognized species emerged from the third collection made at Brighton in 1954 on July 12.

Pimpla aequalis Prov.—Two specimens were obtained on June 24 and 28 from the third collections made at LaSalle and Hepworth in 1955. Adult emergence is also recorded from *Carpocapsa pomonella* L. in Ontario (CNC).

Pimpla turionellae (L.)—One specimen of this species was recovered from the third collection made at Brighton in 1954. This introduced pupal parasite was released at Brighton in 1952 and 1953. The 1954 specimen constitutes the first recovery of the species in the Brighton area from releases made during a previous season.

Scambus hispae complex—This complex includes at least two species, *S. hispae* (Harr.) and *S. tecumseh* Vier., in Ontario. The males of *hispae* and *tecumseh* can be readily distinguished but the females are less easily separated (teste G. S. Walley, Insect Systematics and Biological Control Unit, Ottawa). *S. hispae* is believed to be the more common of the two. Eight specimens of *S. hispae* were obtained from the second and third collections made at Byron, Dunnville, LaSalle, and Roseneath during the survey. Adults emerged between May 24 and July 23.

One specimen of *Scambus* sp. was obtained from the third collection made at St. Williams in 1954, the adult emerging on July 5. Five specimens belonging to this complex emerged from the Brighton collection in late June and early July, 1954, and seven in mid-June in 1955. The life-history and habits of members of this complex are similar to those of *C. comstockii*.

Temelucha sp.—Two specimens were obtained from the second collection made at Dunnville in 1954 and 1956. One specimen was also obtained from St. Williams in 1956. Adult emergence took place between July 9 and July 16.

Temelucha minor (Cush.)—Two specimens emerged on June 9 and 10 from the second collection made at Dunnville in 1955.

Pteromalidae

Habrocytus sp.—One specimen from the third collection made at Elmira emerged on June 21, 1955, and four from the second Dunnville collection emerged on July 3, 1954. Some species of this genus are hyperparasites.

Pteromalini—An unidentified species referred to this tribe emerged from the second collection made at Dunnville on July 28, 1954.

Scelionidae

Telenomus sp.—Although one specimen, taken from a shoot known to be infested by shoot moth, was found in the fourth Perkinsfield collection, it cannot be definitely stated that this is a shoot moth parasite. Members of this genus are known to be parasites of the eggs of various Lepidoptera (Muesebeck *et al.*, 1951).

Others:—Two additional species of parasites have been obtained from the European pine shoot moth in Ontario, but were not found during this or previous surveys: *Madremyia saundersii* (Will.) (CNC), and *Monodontomerus dentipes* (Dalm.) (CNC).

Discussion

Since the European pine shoot moth appeared in Ontario in 1925, 21 indigenous species of hymenopterous parasites have transferred to it from other hosts, most of them occupying similar habitats. Four indigenous species, *Calliephialtes comstockii*, *Hyssopus thymus*, *Eurytoma pini*, and *Itoplectis conquisitor*, and one introduced European species, *Orgilus obscurator*, can be considered as common shoot moth parasites. *Scambus* spp. have also been obtained frequently from shoot moth. The importance of parasitism, about 10 per cent between 1954 and 1956, as a mortality factor of the shoot moth cannot be accurately evaluated at this time.

The changes of, and increase in, the parasite complex attacking the shoot moth as the season advanced was clearly demonstrated by the emergence of the common parasites from the field collections. There was an increase from two species, *H. thymus* and *O. obscurator*, in the first collection to six, *H. thymus*, *O. obscurator*, *C. comstockii*, *E. pini*, *Scambus* spp., and *I. conquisitor*, in the third, or pupal, collection. The number of *O. obscurator* decreased noticeably from the first to the third collections, whereas the numbers of *C. comstockii* and *E. pini* increased from the second to the third collections. These changes agree with observations made by Miller and Neiswander (1955) except that they did not obtain *O. obscurator* in Ohio.

O. obscurator and *H. thymus* were the only common parasites emerging from the first collection of overwintering larvae. The second collection of late-instar larvae and early pupae also contained these species and a few *C. comstockii*, *E. pini*, and *Scambus* spp., which attack mid- and late-stage larvae. The third, or pupal, collection was most heavily parasitized. It contained *H. thymus*, *C. comstockii*, *E. pini*, and *Scambus* spp., species which attack mid- and late-instar larvae and emerge from the pupae; *I. conquisitor*, which attacks the pupae; and a few *O. obscurator*, which sometimes emerge from the pupae. *H. thymus* was the only parasite that emerged from the fourth collection of early-instar larvae.

Dissection of third-instar larvae in August revealed a small number of *O. obscurator* larvae, which would not have emerged until the following spring.

O. obscurator and *Temelucha interruptor* were probably introduced accidentally with the host, for they were found in Toronto and Port Nelson prior to any release of either of these parasites. This suggests that subsequent spread of introduced species of parasites may not be due to release alone, but also to accidental transfer on infested nursery stock.

In 1933 *O. obscurator* was known from 20 and *T. interruptor* from 14 localities in Ontario. The abnormally low winter temperatures of early 1934 killed nearly all the overwintering host larvae and the parasites (*O. obscurator* and *Temelucha* spp., including *interruptor*) that they contained. By 1936, however, the shoot moth was again common and *O. obscurator* was recovered in Toronto, Niagara Falls, and Walkerville, and *T. interruptor* in the first two localities. *O. obscurator* has since been recovered in 14 and *T. interruptor* in six areas. *T. minor* and other unidentified species of *Temelucha* have been obtained since 1954. The distribution of these parasites suggests that *O. obscurator* is generally established where the minimum winter temperature rarely falls below — 10° F., and *Temelucha* spp. where this temperature rarely falls below 0° F.

Other parasites attacking the European pine shoot moth occurred only sporadically. The majority were obtained from the second and third collections.

Because these parasite records were obtained from mass rearings, there may be doubt in some cases that the parasites were actually associated with the shoot moth. There can be no doubt about *Calliephialtes comstockii*, *Eurytoma pini*, *Hyssopus thymus*, *Itoplectis conquisitor*, *Orgilus obscurator*, *Scambus* spp. because all were obtained in reasonably large numbers from many areas. Although only a few specimens were obtained of *Habrocytus* sp., *Itoplectis evetriae*, and *Pimpla turionellae*, they are probably shoot moth parasites since they have been recorded as such elsewhere (Muesebeck *et al.*, 1951; Thompson, 1947). Only single specimens or short series were obtained of *Campoplex* sp., *Temelucha* sp., *Gelis* sp., *Phaeogenes* sp., *Pimpla aequalis*, *Elachertus* sp., *Atrometus clavipes*, and *Eupelmella vesicularis*, so that further rearing is required to associate these species positively with the shoot moth.

Acknowledgments

The authors wish to acknowledge the assistance and helpful criticism of various officers at the Sault Ste. Marie and Belleville laboratories, especially R. M. Belyea, B. P. Beirne, and J. H. McLeod.

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(Received April 7, 1959)

Revision of the Genus *Linosta* Möschler (Lepidoptera: Pyralidae)[1] with Characterization of the Subfamily Linostinae and a New Subfamily

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The genus *Linosta* was described by Möschler (1881: 433) for the single species *L. sinceralis* Möschler from Surinam. There have been few subsequent published references to the genus, but in most collections it stands in the Schoenobiinae. Amsel (1956) surveyed the structural characters and noted that the genus did not fit very well into the Schoenobiinae or any other subfamily and that it would possibly require its own subfamily "Linosterinae", but he left it in Schoenobiinae for the time being. In my opinion the group is sufficiently distinguished from the Schoenobiinae by the absence of proboscis, of maxillary palpus, of chaetosema, and of tubular 1st A of primary, as well as by the different tympanic and genital structure. The absence of the maxillary palpus would place the genus in Chrysauginae, but the joining of the tympanic bullae and the presence of a definite praecinctorium (new term for tablier of Guenée = Schürze of Lederer = Kielhäutchen of Amsel) rule this out. The group obviously belongs in the basal part of the crambine-pyraustine complex; the actual affinity appears to be to the Cybalomiinae (new subfamily, type genus *Cybalomia* Lederer, characters of Crambinae, but with chaetosema absent). The male genitalia agree well with those of *Cybalomia* and *Stiphrometasia*, especially in the close association of the base of the gnathos with a strap-like sclerite connecting with the costal articulation of the valve. Also the tympanic structure is closely similar to that of *Stiphrometasia* and furthermore to that of *Thyridophora*, which has a fovea and associated stalking of R_5 and M_1, just as in *Linosta*, and which also lacks the proboscis. Unfortunately I have dissected only the female of *Thyridophora*, and do not know whether the structure of the male genitalia supports the other resemblances. However, I think the abortion of the maxillary palpus and great reduction of the labial palpus is a sufficiently important character to require the erection of a distinct and probably unigeneric subfamily, which I call Linostinae (emendation of Linosterinae Amsel), type genus *Linosta* Möschler.

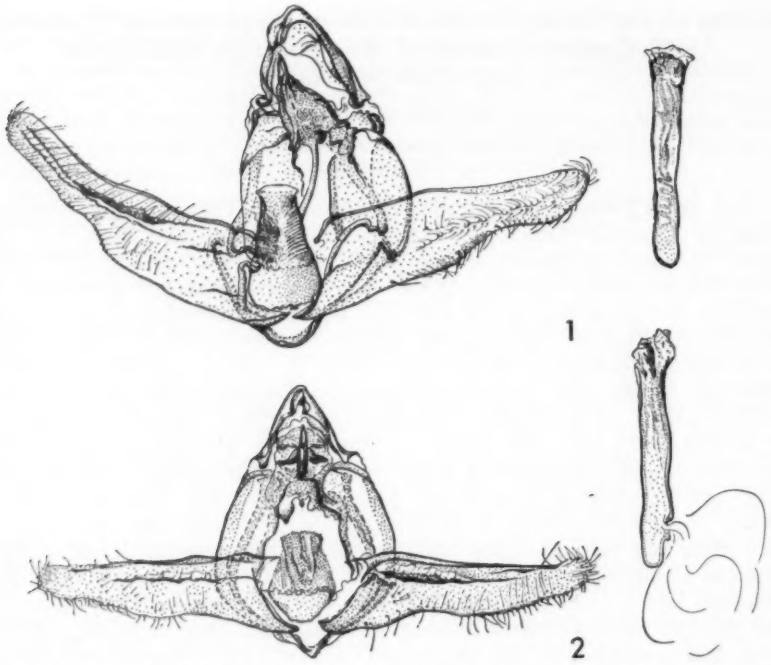
The genus is entirely Neotropical, ranging from Mexico to Bolivia and southern Brazil. There appear to be two species, one undescribed. The described species is divisible into several subspecies.

Linosta annulifera, new species

Figs. 1, 3

This species is closely similar to *Linosta sinceralis* in external appearance, except that the discal marking of the forewing is a large, almost complete ring, not a closely approximated pair of dashes or dots. The size is as large as in the largest specimens of *L. sinceralis* and the dark markings are heavier than in most specimens of that species. The abdomen has a black mid-dorsal basal spot and six heavy transverse black bars on the dorsa of succeeding segments. The male has the gnathos heavier and longer than in *L. sinceralis*, forming a single claw-like structure, rather than a transverse element with a central carina and tooth. The new species occurs in Peru and Bolivia, and is largely allopatric to *L. sinceralis;*

[1]Contribution No. 3936, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.



Figs. 1, 2. *Linosta* spp., ♂ genitalia. 1, *L. annulifera* Munroe; 2, *L. sinceralis* Möschler.

both species are recorded from the Carabaya district of Peru, but *L. annulifera* from high altitudes and *L. sinceralis* from low.

Holotype, male, Oconeque, S.E. Peru, July, 1904, 7,000 ft., G. Ockenden. Type No. 6576, Canadian National Collection, ex coll. E. Munroe, purchased from W. F. H. Rosenberg.

Allotype, female, Uruhasi, S.E. Peru, 7,000 ft., "4-5.'10", H. and G. Watkins, in the British Museum (Natural History), London.

Paratypes. 47 specimens from the following localities: Peru: Oconeque; Quinton, and Aqualani; Bolivia: Cochabamba, Yungas de Arepucho, and Yungas de La Paz.

Paratypes in the C.N.C., British Museum (Natural History), Carnegie Museum, Pittsburgh, and Bavarian State Zoological Collection, Munich.

***Linosta sinceralis* Möschler**

Fig. 2

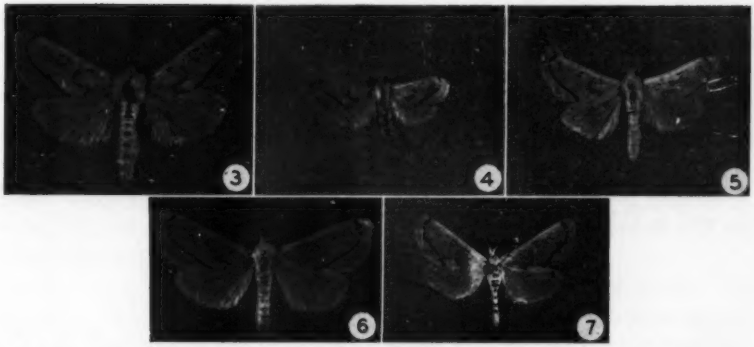
Linosta sinceralis Möschler, 1881: 433, Pl. 18, Fig. 40.

This species differs externally from *L. annulifera* in having the discal marking of the forewing composed of a pair of small, parallel lines or absent, and genitalically in the much more slender and delicate gnathos. The species varies geographically, and I recognize four subspecies.

***Linosta sinceralis sinceralis* Möschler**

Fig. 4

This is the smallest subspecies, males ranging in wing-span from 23 to 25 mm. The discal marking of the forewing consists of a pair of minute black dots or



Figs. 3-7. *Linosta* spp. 3, *L. annulifera* Munroe; 4, *L. sinceralis sinceralis* Möschler; 5, *L. s. centralis* Munroe; 6, *L. s. andina* Munroe; 7, *L. s. plaumanni* Munroe.

dashes, one or both of which may be lacking. In a few specimens the veins are contrastingly dark. I have not seen this condition in other subspecies. The abdomen is weakly marked, the first three or four transverse bands being more distinct than those behind.

I have seen typical material from British, French and Dutch Guiana, from the lower, middle and upper Amazons as far as Fonteboa, and from the Rio San Francisco and Bahia, Brazil. Specimens from western Venezuela are atypical, averaging a little larger, and some having the abdomen heavily banded with black, but they are best referred here.

Material examined: 33 specimens, including nine from Venezuela.

***Linosta sinceralis centralis*, new subspecies**

Fig. 5

Larger than the nominate subspecies, males ranging from 25 to 35 mm. in expanse. Discal markings as in the nominate subspecies, rarely completely lacking, and this usually in females; black abdominal markings much reduced, usually consisting of a narrow transverse line, preceded by two pairs of dots and followed by a partial transverse line.

This subspecies occurs throughout Central America.

Holotype, male, and allotype, female, Finca "La Violeta", Soconusco, Chiapas, Mexico, 850 m., Aug. 24 and Oct. 2, 1954, type No. 6577, C.N.C.

Paratypes. 32 specimens, from the following localities:

Mexico: Finca "La Violeta", Soconusco, Chiapas; Jalapa; Orizaba; Tabasco; Coatepec.

Guatemala: Quirigua; Senahu, Vera Paz.

Costa Rica: Juan Vinas; San José; Candelaria Mts.; Tuis; San Carlos; Carreblanco; Sixola R.; Sitio; Irazu, 6-7,000 ft.

Paratypes in the C.N.C., American Museum of Natural History, Carnegie Museum, Berlin Museum, Bavarian State Zoological Collection, and British Museum (Natural History).

***Linosta sinceralis andina*, new subspecies**

Fig. 6

Similar in size to *L. s. centralis*, and with the abdominal markings likewise reduced; discocellular markings of forewing usually absent, rarely weakly expressed.

Holotype, female, Balzapamba, Prov. Bolivar, Ecuador; allotype, male, Colombia, A. E. Pratt; both in British Museum (Natural History).

Paratypes. 17 specimens, from the following localities:

Colombia: no exact locality.

Ecuador: Balzapamba; La Chima, Prov. del Rios; Baños.

Peru: La Union, Rio Huacamayo, Carabaya, 2,000 ft.; Moychambo; Irazu.

Paratypes in British Museum (Natural History), in Zoological Museum, Berlin, and in C.N.C., type No. 6578.

***Linosta sinceralis plaumanni*, new subspecies**

Fig. 7

Larger than the nominate subspecies, but much smaller than *L. s. centralis* or *L. s. andina*. Dorsal markings of abdomen strongly developed; both parenthesis-like discocellular markings of forewing usually present; anterior rudiment of post-medial line of under side of hind wing better developed than in more northerly subspecies.

Holotype, male, and allotype, female, Nova Teutonia, Sta. Catharina, Brazil, F. Plaumann, type No. 6579, C.N.C.

Paratypes. 17 specimens from:

Brazil: Nova Teutonia, Sta. Catharina; Nova Bremen, Sta. Catharina; Corupá, Sta. Catharina; Rio Natal, Sta. Catharina; Alto de Serra, São Paulo; Petrópolis, R.deJ.; Januaria, Minas Geraes; Cariuhuaha, Minas Geraes; Burity, 30 mi. E. of Cuyaba, Matto Grosso, 2,250 ft.

Summary

The genus *Linosta* is considered to belong to a separate subfamily, Linostinae Amsel, emend., related to the Cybalomiinae, new subfamily. These subfamilies are defined. Two species of *Linosta* are recognized: *L. annulifera*, n. sp., from Peru and Bolivia, and *L. sinceralis* Möschler. The latter is divided into four subspecies: the nominate subspecies from the Guianas, the Amazons and possibly Venezuela; *L. s. centralis*, n. sp., from Central America; *L. s. andina*, n. sp., from Ecuador, Colombia and Peru; and *L. s. plaumanni*, n. sp., from Southern Brazil.

Acknowledgments

I am much indebted to the authorities of the British Museum (Natural History), and particularly to Mr. E. L. Martin, formerly of that institution, to Dr. Walter Forster, Bavarian State Zoological Collection, Munich, and to Mr. Harry K. Clench, Carnegie Museum, Pittsburgh, for the loan and gift of material.

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(Received March 24, 1959)

Gall Aphids on Poplar in Alberta
I. Descriptions of Galls and Distributions of Aphids[1]

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No research has previously been conducted on gall aphids on poplar in Alberta. Strickland (1953) published records of some of these aphids in his list of Hemiptera of Alberta. Manson (1931) mentioned that noctuids fed in galls of *Pemphigus populitransversus* Riley.

In the United States, several workers have reported on these aphids. Palmer (1952, pp. 358-372) published a key to and some biological notes on several species of the genus *Pemphigus* and related genera. Maxson and Knowlton (1929) gave considerable information on the life-history and classification of the tribe Pemphigini. Maxson (1923) and Hottes and Frison (1931) published keys to the same tribe. Essig (1926, pp. 259-261), Gillette (1913), Gillette and Bragg (1915), Jackson (1908), Oestlund and Hottes (1926), Patch (1913), Swaine (1919), and Williams (1910) also reported on some of the gall aphids on poplar.

Although several of these aphids are economically important on their secondary hosts, the sugar-beet root aphid, *Pemphigus betae* Doane, is the only one of importance in Alberta at present.

Occasionally invaginations that appear to be galls are found in leaves; these depressions are galls in the early stage of development in which the fundatrices have died. The gall develops fully only when the aphid is present.

Galls of more than one species were observed in southern Alberta on a single tree, branch, or leaf, and occasionally more than one gall of a species on a single leaf. Figs. 14-20 show some of these associations of galls.

This paper deals with descriptions of the galls of aphids on poplar and with distribution records of these aphids in Alberta.

Key to Galls

1. Gall on *Populus sargentii* Dode 2
   Gall on other species of poplar 7
2. Gall on new growth of twig (Fig. 6) ..... *Pemphigus populiramulorum* Riley
   Gall on leaf or terminal bud 3
3. Gall formed from terminal bud, convoluted, bladder-like (Figs. 9 and 10) ..... *Mordwilkoja vagabunda* (Walsh)
   Gall on leaf 4
4. Gall on petiole 5
   Gall at junction of petiole and leaf blade 6
5. Gall with transverse slit (Fig. 4) ..... *Pemphigus populitransversus* Riley
   Gall with angular slit formed by twisting and swelling of petiole (Fig. 20) ..... *Pemphigus nortonii* Maxson
6. Gall formed by swelling and twisting of petiole and leaf blade (Figs. 3, 19) ..... *Pemphigus populicaulis* Fitch
   Gall formed by swelling and twisting of petiole only (Fig. 5) ..... *P. nortonii* Maxson
7. Gall formed by swelling and twisting of petiole and leaf blade of *Populus angustifolia* James or *Populus balsamifera* L. (or, rarely, *Populus trichocarpa* T. and G.) (Fig. 2) ..... *Pemphigus populiglobuli* Fitch
   Gall on leaf blade 8
8. Gall beside mid-rib on upper side of leaf of *P. balsamifera* (Fig. 7) ..... *Pemphigus populivenae* Fitch
   Gall on underside of leaf 9

[1]Contribution No. 112, Science Service Laboratory, Canada Department of Agriculture, Lethbridge, Alberta; from a thesis submitted in partial fulfillment of the requirements for the Ph.D. degree, Washington State College, 1957.
[2]Associate Entomologist.

9. Gall beside mid-rib on leaf of *P. balsamifera* or *P. angustifolia* (or, rarely, *P. trichocarpa*) (Fig. 1) ..... *Pemphigus betae* Doane
Row of galls on either side of mid-rib of *P. angustifolia* or *P. balsamifera* (Fig. 8) ..... *Thecabius populimonilis* (Riley)

Pemphigus betae Doane

This species, which is a pest of beets, swiss chard, spinach, and lettuce, causes considerable damage each year to sugar beets in southern Alberta and in some areas of the United States. *P. betae* can spread curly top virus and virus yellows among sugar-beet plants (Bennett and Wallace, 1938; MacLean, 1953).

The galls are always on the leaf blades, usually next to the mid-ribs; generally there is only one per leaf. They have been found in Alberta on the narrow-leaved cottonwood, *P. angustifolia;* the balsam poplar, *P. balsamifera;* and, rarely, the black cottonwood *P. trichocarpa.* The fundatrix, which hatches from the overwintered egg, feeds near the mid-vein on the upper surface of the emerging leaf, causing the formation of a longitudinal depression, which increases in size to about half an inch long and a quarter of an inch deep (Fig. 1). Galls are usually green but may have a reddish tinge.

Records of the distribution of *P. betae* in Alberta are as follows (the year denotes the first record from the area): 1929, Picture Butte, beets, lamb's-quarters, pigweed; 1934, Lethbridge(Hillspring, Barnwell, beets (MacNay, C. G. (in litt.) Entomology Division, Ottawa); 1950, Monarch, Coaldale, Magrath, Raymond, *Beta vulgaris, Chenopodium album,* poplars; 1954, Diamond City; 1956, Pincher Creek, Barons, Hays, Turin, Welling, Stirling, beets, lettuce, *Populus balsamifera, P. angustifolia, P. trichocarpa;* 1957, Lundbreck, Black Diamond, Coleman, poplars.

Pemphigus populiglobuli Fitch

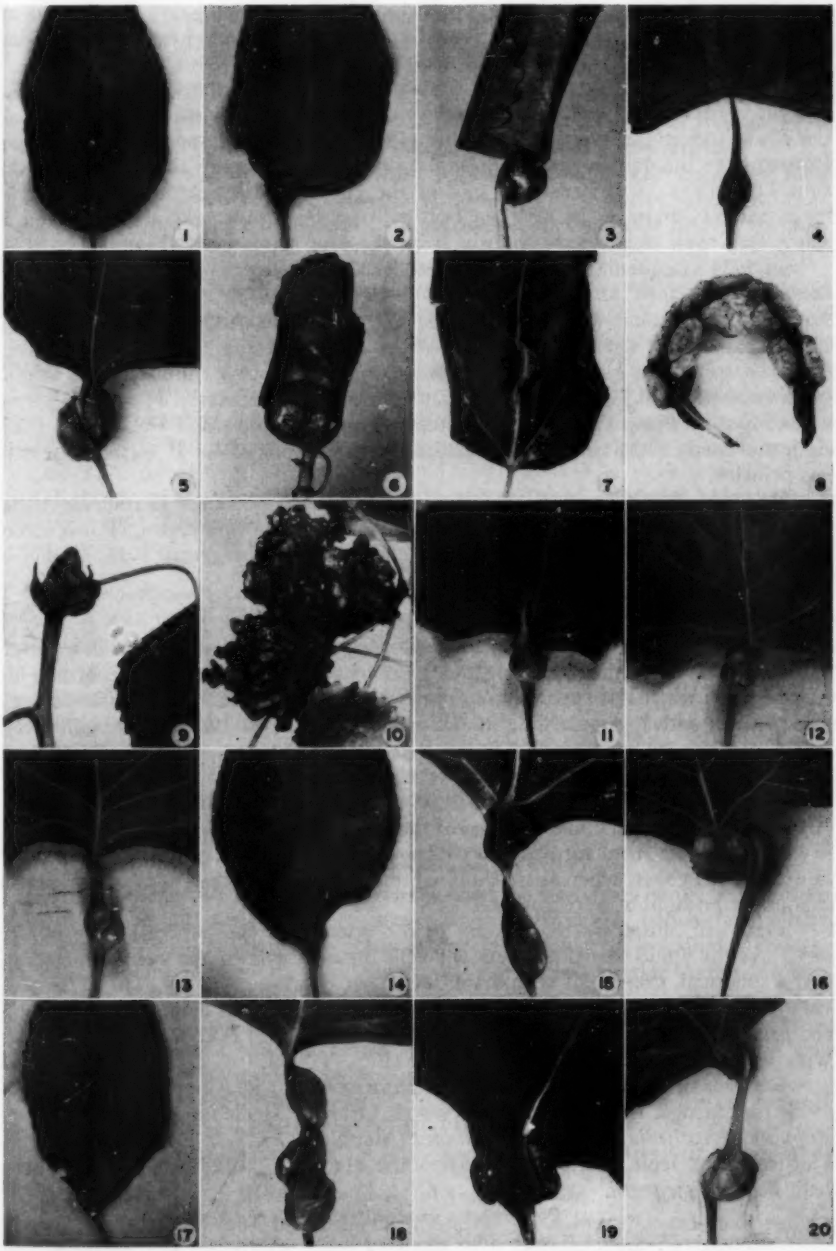
The primary hosts of *P. populiglobuli* in Alberta are *P. angustifolia, P. balsamifera,* and, rarely, *P. trichocarpa.* The gall is formed at the junction of the petiole and leaf blade and is produced by a swelling at the base of the blade and at the top of the petiole (Fig. 2). The exit slit is produced by a slight separation of the twisted parts of the petiole and blade. Usually the gall is green but it may have a reddish tinge.

Records of the distribution of *P. populiglobuli* in Alberta are as follows: 1954, Lethbridge, Magrath, Cardston, Coaldale, Picture Butte, *P. angustifolia, P. balsamifera;* 1957, Pincher Creek, Black Diamond, Lundbreck, Coleman, Blairmore, Crowsnest, Cyprus Hills, Medicine Hat, Waterton, Monarch, Macleod, *P. balsamifera, P. angustifolia, P. trichocarpa.*

These figures show galls at approximately half normal size.

Figs. 1-10. Galls caused by aphids on poplar in southern Alberta. 1, by *Pemphigus betae* Doane on the underside of a leaf of *Populus balsamifera;* 2, by *P. populiglobuli* Fitch on a leaf of *P. balsamifera;* 3, by *P. populicaulis* Fitch on a leaf of *P. sargentii;* 4, by *P. populitransversus* Riley on a leaf of *P. sargentii;* 5, by *P. nortonii* Maxson on a leaf of *P. sargentii;* 6, by *P. populiramulorum* Riley on a twig of *P. sargentii;* 7, by *P. populivenae* Fitch on the upper side of a leaf of *P. balsamifera;* 8, by *Thecabius populimonilis* (Riley) on a leaf of *P. angustifolia;* 9, by *Mordwilkoja vagabunda* (Walsh) on terminal bud of *P. sargentii* (early stage of gall); 10, by *M. vagabunda* on *P. sargentii* (fully developed gall).

Figs. 11-20. 11-13, galls of *P. populitransversus* with vertical and angular slits; 14, gall of *P. betae* and one of *P. populiglobuli* on leaf of *P. balsamifera;* 15, gall of *P. populicaulis* Fitch and one of *P. populitransversus* Riley on the same leaf; 16, gall of *P. populicaulis* Fitch and one of *P. nortonii* on the same leaf; 17, three galls of *P. betae* Doane on the same leaf; 18, three galls of *populitransversus* on the same leaf; 19, two galls of *P. populicaulis* on the same leaf; 20, two galls of *P. nortonii* on the same leaf.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***Pemphigus populicaulis* Fitch**

P. populicaulis is more common in southern Alberta than any other gall-forming aphid on poplar. The galls are found on trees along river banks and in many of the shelter belts in the irrigated areas. The primary host of this species in Alberta is *P. sargentii* Dode.

The gall caused by this aphid is also formed at the junction of the petiole and blade of the leaf and is produced by a swelling and twisting at the base of the blade and at the top of the petiole (Fig. 3). In this respect it is similar in formation to the gall caused by *P. populiglobuli* but differs in that it has a small, round exit (Fig. 19) whereas the exit of the gall caused by *P. populiglobuli* is a long, narrow, angular slit. When two galls of *P. populicaulis* are found on a single leaf, their shapes vary slightly from those of single galls (Fig. 19).

In 1924 Glendenning reported water parsley, *Oenanthe sarmentosa* Presl, as the secondary host of *P. populicaulis*. Strickland (1953) recorded *Pemphigus brevicornis* Hart. from potatoes, beets, and celery in August and September. Hottes and Frison (1931) collected *P. brevicornis* on roots of an umbrella plant, *Erigeron* sp., and a goldenrod, *Solidago* sp., and stated that the specimens might be the sexuparae of *P. populicaulis*. Cutright (1925) considered *P. brevicornis* as a synonym of *Pemphigus lactucae* Fitch. Thus, if Hottes and Frison and Cutright are correct, the name *P. populicaulis* will be replaced by *P. lactucae*, which has priority.

Records of the distribution of *P. populicaulis* in Alberta are as follows: 1950, Picture Butte, Lethbridge, Coaldale, Taber, Vauxhall, Grantham, Turin, Iron Springs, Monarch, Macleod, Barnwell, Welling, *Populus sargentii;* 1953, Medicine Hat; 1957, Nobleford, *Populus sargentii.*

***Pemphigus populitransversus* Riley**

P. populitransversus occurs on *Populus sargentii* in some localities along river banks and in shelter belts in irrigated areas of southern Alberta. According to MacNay (in litt.), this species was reported occasionally on *Populus deltoides*, *P. tremuloides*, and *P. angustifolia* in Alberta from 1929 to 1957. Although Essig (1926, pp. 259-261) indicated that this species may live on sugar beets, dock, and lettuce, it has not been found on these hosts in Alberta. Wene and White (1953) stated that *P. populitransversus* is an important pest of cabbage in Texas. Although no secondary host has been found in Alberta, winged forms were taken in large numbers from turnips and cabbage in plots at the Lethbridge laboratory in 1954. However, when these plots were harvested and the roots of the plants examined, no aphids were found.

Galls are caused by the feeding of this species on the petiole of the poplar leaf. As the aphid feeds, the petiole swells on each side of the point of feeding and a spherical, green gall with a transverse slit is produced (Fig. 4). The galls vary in size from one-quarter to three-quarters of an inch in diameter. Although the galls generally have transverse slits, some were found near Cranford, Alberta, with vertical, transverse, or angular slits (Figs. 11-13).

Records of the distribution of *P. populitransversus* in Alberta are as follows: 1929, Lethbridge, Bow River, Arrowwood, Orkney, Macleod, *Populus deltoides*, *Populus angustifolia*, *Populus tremuloides* (MacNay, C. G. (in litt.)); 1950, Turin, Picture Butte, Iron Springs; 1953, Medicine Hat; 1957, Barnwell, Taber, Vauxhall, *Populus sargentii.*

***Pemphigus nortonii* Maxson**

Although *P. nortonii* was first reported from southern Alberta only four years ago, now it can be readily found on *P. sargentii* in shelter belts and on trees along river banks. As yet no secondary host has been recorded for this species.

The gall is formed on the petiole or at the junction of the leaf blade and the petiole and is produced by a swelling and twisting of the petiole only (Fig. 5). Although the gall is somewhat similar to that caused by *P. populicaulis*, it is generally larger, often growing to three-quarters of an inch or more in diameter. The exit from the gall is a long, semispiral slit and not a small, round opening as with *P. populicaulis*.

Records of the distribution of *P. nortonii* in Alberta are as follows: 1953, Grantham; 1957, Taber, Turin, Lethbridge, Coaldale, *Populus sargentii*.

This aphid was originally reported by the author in The Canadian Insect Pest Review (MacNay, 1955) as *Pemphigus junctisensoriatus* Maxson. Since then Maxson has checked the material and identified the aphid as *P. nortonii*.

***Pemphigus populiramulorum* Riley**

Very few galls of *P. populiramulorum* were found in Alberta. This aphid was first reported in the area in 1954 and since then a few galls were found each year. The gall (Fig. 6) is formed not on the leaf but on the new growth of the twig; as the aphid feeds, the twig swells and encloses it. The gall is round and has a transverse or vertical slit similar to that in the gall of *P. populitransversus* but with protruding lips. It is greenish at first but turns brown as the season progresses. In fall it remains on the tree and thus may be easily seen during the winter or early spring.

Records of the distribution of *P. populiramulorum* Riley in Alberta are as follows: 1954, Grantham, *Populus sargentii;* 1956, Taber, Coaldale, *P. sargentii*.

***Pemphigus populivenae* Fitch**

P. populivenae occurs in Alberta in very small numbers. In every locality where it was found in Alberta it was associated with galls caused by *P. betae* or *P. populiglobuli*. This species feeds close to the mid-rib on the undersides of the leaves of *P. angustifolia* or *P. balsamifera*, causing a gall (Fig. 7) about one-quarter to one-half of an inch long and about a quarter of an inch deep on the upper side of the leaf. The gall is similar to that of *P. betae* but is on the opposite side of the leaf.

Records of the distribution of *P. populivenae* in Alberta are as follows: 1953, Edmonton (Strickland, 1953), Monarch, *P. angustifolia, P. balsamifera;* 1957, Lundbreck, Coaldale, *P. balsamifera*.

***Thecabius populimonilis* (Riley)**

T. populimonilis is found on small trees along river banks in southern Alberta. The hosts of this species are *P. angustifolia* and *P. balsamifera*.

The galls of this species do not contain colonies but only a single fundatrix or fundatrigenia. The fundatrix causes the gall, in which the young are produced, but shortly after the young are born they leave the gall and start to feed on the same leaf or on another leaf, causing galls to be produced at the point of feeding, usually in a row on either side of the mid-rib. The galls are pale green but may have a reddish tinge (Fig. 8).

Records of the distribution of *T. populimonilis* in Alberta are as follows: 1948, Elk Island Park (Strickland, 1953); 1951, Lethbridge, *Populus angustifolia;* 1956, Monarch, Picture Butte, *P. angustifolia;* 1957, Spirit River, *P. balsamifera*.

***Mordwilkoja vagabunda* (Walsh)**

The largest and most unusual gall on poplar in southern Alberta is caused by *M. vagabunda*. The primary host in the area is *Populus sargentii*.

The gall caused by this species is usually large and conspicuous. The feeding of the fundatrix on the terminal bud results in the formation of a bladder-like

gall. Fig. 9 shows the early stage of one of these galls and Fig. 10 the fully developed, convoluted gall. In autumn the galls do not fall but turn woody and remain on the tree the following year.

Distribution of *M. vagabunda* in Alberta is as follows: 1930, southern Alberta, *Populus* species (MacNay, C. G. (in litt.)); 1948, Rocky Mountain House (Strickland, 1953); 1955, Grantham, *Populus sargentii;* 1957, Turin.

Discussion

Records of distributions of these species are valuable because of the economic importance of some of the aphids on secondary hosts. The importance of *Pemphigus betae* Doane and *P. populitransversus* Riley has already been discussed. A European species that has not been recorded from Alberta but that may become important in Canada is the lettuce-root aphid, *Pemphigus bursarius* (L.). It is a pest of lettuce in California (Lange *et al.*, 1957). In personal correspondence Dr. W. H. Lange, Entomology Department, University of California, Davis, California, stated that in 1956 he found galls of *P. bursarius* to be common in the region of Ottawa, Ontario.

This paper provides evidence that the point of feeding on the leaf is not the only factor determining the type of gall formed by an aphid. The species *P. populitransversus* and *P. nortonii* (Figs. 4, 5) may both produce galls anywhere on the petiole of a leaf of *P. sargentii.* The feeding of *P. nortonii* causes a swelling and twisting of the petiole whereas that of *P. populitransversus* causes the petiole to swell only. The difference in gall formation may be due to feeding of the aphids on different tissues or to the injection of different plant growth stimulants.

As the galls of most of these species age, they seem to develop a type of differential stress that causes them to open sufficiently for the escape of the migrants. The gall of *M. vagabunda* is unusual in that it is completely closed until shortly before the fundatrigeniae are ready to migrate. At that time the ends of the small projections on the gall become dry and split open, leaving exits for the aphids.

Observations on growth of galls indicated that, in the genus *Pemphigus*, only the fundatrix can cause galls to develop for once she is fully developed the gall does not increase in size, even though the galls are full of her offspring, the fundatrigeniae. In the aphid *Thecabius populimonilis*, however, the fundatrigeniae are also capable of initiating gall formation. On galls caused by the species *Mordwilkoja vagabunda*, knobby protuberances occur when the fundatrigeniae begin to feed and develop. As the gall is closed at that time, the fundatrigeniae cannot escape to form a new gall, but they appear to be able to stimulate growth of the gall they are inhabiting.

In southern Alberta there occur numerous hybrids of the four common species of poplar: *P. sargentii*, *P. angustifolia*, *P. balsamifera*, and *P. acuminata.* Galls of *P. betae*, *P. populiglobuli*, *P. populivenae*, and *T. populimonilis* are found on *P. angustifolia* or *P. balsamifera* or hybrids of *P. angustifolia* and *P. balsamifera.* Occasionally *P. betae* and *P. populiglobuli* were found near Lethbridge on *P. angustifolia* X *P. acuminata* hybrids. Galls of *P. populicaulis*, *P. nortonii*, *P. populitransversus*, *P. populiramulorum*, and *M. vagabunda* are found on *P. sargentii.* Near Turin, *P. populicaulis* and *M. vagabunda* were found on a hybrid of *P. sargentii* X *P. acuminata.* Evidently, therefore, the aphids can be separated into two groups on the basis of hosts. *P. acuminata* hybrids, however, appear to form a link between the two groups.

Summary

A key is given for the separation of galls caused by nine poplar gall aphids from southern Alberta, *Pemphigus betae* Doane, *P. populiglobuli* Fitch, *P. populivenae* Fitch, *Thecabius populimonilis* (Riley), *Pemphigus populicaulis* Fitch, *P. populitransversus* Riley, *P. nortonii* Maxson, *P. populiramulorum* Riley, and *Mordwilkoja vagabunda* (Walsh). The narrow-leaved cottonwood, *Populus angustifolia* James, and the balsam poplar, *P. balsamifera* L., are primary hosts of the first four species listed whereas *P. sargentii* Dode is the primary host of the last five. In the species *T. populimonilis* both the fundatrix and the fundatrigeniae can initiate gall formation whereas in *M. vagabunda* the fundatrix initiates gall formation and the fundatrigeniae appear to be able to cause the gall to increase in size. In the other species studied, only the fundatrix can initiate gall formation and cause the galls to enlarge. Galls caused by *P. betae*, *P. populiglobuli*, *P. nortonii*, and *P. populicaulis* are common in southern Alberta, and galls of *M. vagabunda*, *T. populimonilis*, and *P. populitransversus* can be found on a few trees each year, whereas galls of *P. populivenae* and *P. populiramulorum* are rare.

P. betae is the only one of the aphids studied that is of economic importance in Alberta. It lives on the roots of sugar beets during the summer and causes considerable damage to that crop.

Acknowledgments

The writer wishes to thank Mr. A. C. Maxson, Longmont, Colorado, for checking the identification of the aphids, officers of the Crop Insect Section, Lethbridge, and Mrs. Jean B. Adams, Entomology Laboratory, Fredericton, N.B., for criticisms and suggestions during the writing of the manuscript.

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(Received February 5, 1959)

Estimation of Parasitism of Larch Sawfly Cocoons by *Bessa harveyi* Tnsd. in Survey Collections[1]

By W. G. H. Ives and R. M. Prentice[2]

Introduction

The Forest Insect Survey at the Forest Biology Laboratory, Winnipeg, has been compiling records for a number of years on the percentage of cocoons of the larch sawfly, *Pristiphora erichsonii* (Htg.), parasitized by the tachinid *Bessa harveyi* Tnsd. Sawfly cocoons were collected each fall from the soil in infested stands, and those containing living larvae were dissected to determine the percentage of parasitism by *B. harveyi*. These estimates have been used to provide an index of parasitism (Lejeune and Hildahl, 1954), but are of limited value for a number of reasons: (1) estimates can be expressed only as percentage of sound cocoons parasitized; (2) total parasitism cannot be estimated because a portion of the parasites emerge from the cocoons before collection; and (3) estimates of parasitism may not be representative of the stand because there is a tendency to collect cocoons where they are easiest to find; hence all the cocoons in a collection may be from one or two small areas. If the proportion of cocoons containing *B. harveyi* varies within a stand such collections may give unreliable estimates of parasitism.

A change in the method of cocoon collection is therefore being planned. Cocoons will be obtained by placing a number of four-square-foot trays containing moss under the crowns of trees to catch the sawfly larvae as they fall. Cocoons will be collected from the trays in late September. This method will provide counts of the total number of cocoons formed, and of the number of fall emerging *B. harveyi*. It will therefore be possible to estimate the total parasitism as a percentage of the number of cocoons formed.

The authors are indebted to W. J. Turnock and R. J. Heron of the Forest Biology Laboratory, Winnipeg, for some of the data used in this paper.

Intra-Plot Variation in Parasitism

Before designing a cocoon collecting program, available data were examined to determine the best method for positioning the trays in the bogs. Parasite records were available from an intensive study conducted in the Whiteshell Forest Reserve, Manitoba, in 1957. Cocoons were collected from 277 randomly located traps in a half-acre plot. The plot was divided into 12 equal sub-plots to determine the intra-plot variability in parasitism by *B. harveyi*. The proportion parasitized varied from .240 to .347, which was a highly significant difference

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TABLE I

Summary of data on parasitism of larch sawfly cocoons by *B harveyi*

Source of data	No. of samples (n)	No. of cocoons per sample ($\bar{x}$)	No. of cocoons per sq. ft.	Proportion parasitized (p)	Variance of p v(p)
Whiteshell, Group I, 1956	15	196.5	12.68	.1927	.00036
Whiteshell, Group I, 1957	15	364.9	23.54	.2203	.00055
Whiteshell, Group II, 1957	10	330.5	21.32	.2844	.00012
Whiteshell, Group III, 1957	10	63.6	31.80	.3726	.00132
Whiteshell, Group IV, 1957	277	25.1	12.55*	.2802	.00004
Pierceland, 1955	16	13.0	3.25	.0144	.00008
Pierceland, 1956	14	9.1	2.28	.1260	.00087
Pierceland, 1957	18	11.7	2.92	.1571	.00037
The Pas, 1958	20	14.1	3.52	.5319	.00116
Cranberry Portage, 1958	20	15.1	3.78	.2853	.00185

*Based on random location of traps, hence is not comparable to other collections where traps were placed beneath crowns of trees.

(chi-square equals 30.68, with 11 degrees of freedom). The trays should therefore be scattered throughout each plot, not concentrated along one edge or in one area because of easy accessibility.

Number of Sampling Units

Because of the high cost of materials and the time involved in hand picking and sorting of the moss, the number of trays that can be used for collecting cocoons in study plots is limited. Available data on *B. harveyi* parasitism were used for estimating the variance of p and sample sizes for a given degree of accuracy.

The formula for estimating the variance in a Binomial distribution is not applicable to data collected in groups (Cochran, 1953). The correct formula for such data, neglecting the finite correction, is

$$v(p) = \frac{1}{n(n-1)\bar{x}^2}\left[\sum_{i=1}^{n} y_i^2 + p^2 \sum_{i=1}^{n} x_i^2 - 2p \sum_{i=1}^{n} y_i x_i\right]$$

where n is the number of sampling units; y_i is the number of cocoons parasitized by *B. harveyi* in the i^{th} sampling unit; x_i is the number of sawfly cocoons in the i^{th} sampling unit; $\bar{x} = \left(\sum_{i=1}^{n} x_i\right)/n$ is the mean number of cocoons per sampling unit; and $p = \left(\sum_{i=1}^{n} y_i\right) \Big/ \left(\sum_{i=1}^{n} x_i\right)$ is the proportion of cocoons parasitized by *B. harveyi*. This and subsequent formulas are all given by Cochran (1953) but are repeated here for clarity of presentation. The above formula was used to calculate the variances of p for the groups of data (Table I). An equivalent formula, again ignoring the finite correction, is

TABLE II

Estimated sample sizes (n_o) and relevant data for estimating parasitism of larch sawfly cocoons by *B. harveyi*

Source of data	C_{yy}	C_{xx}	C_{yx}	Class interval for p	d = .05		d = .10	
					$cv(p_o)$*	n_o	$cv(p_o)$*	n_o
Whiteshell, Group I, 1956	0.6328	0.3960	0.4425	.10–.20	.167	6	.334	2
Whiteshell, Group I, 1957	0.8916	0.4383	0.5798	.20–.30	.100	17	.200	5
Whiteshell, Group II, 1957	0.1815	0.2010	0.1834	.20–.30	.100	2	.200	1
Whiteshell, Group III, 1957	0.8103	0.5738	0.6444	.30–.40	.071	19	.142	6
Whiteshell, Group IV, 1957	0.6759	0.5409	0.5335	.20–.30	.100	16	.200	4
Pierceland, 1955	8.4139	0.8245	1.6684	0–.10	.500	24	1.000	6
Pierceland, 1956	3.5166	1.7639	2.2545	.10–.20	.167	28	.334	7
Pierceland, 1957	1.5489	1.0571	1.1688	.10–.20	.167	10	.334	2
The Pas, 1958	1.2566	1.2680	1.2214	.50–.60	.045	41	.091	10
Cranberry Portage, 1958	0.8367	1.0724	0.6727	.20–.30	.100	56	.200	14

*The coefficients of variation of p at the mid-point in class interval, p_o, which gave the half confidence interval width, $|d|$, as specified. These values of $cv(p_o)$ are used in the calculations for estimating sample size.

$$v(p) = \frac{p^2}{n}[C_{yy} + C_{xx} - 2C_{yx}]$$

$$\text{where } C_{yy} = \sum_{i=1}^{n} (y_i - \bar{y})^2/(n-1)\bar{y}^2$$

$$C_{xx} = \sum_{i=1}^{n} (x_i - \bar{x})^2/(n-1)\bar{x}^2$$

$$C_{yx} = \sum_{i=1}^{n} (x_i - \bar{x})(y_i - \bar{y})/(n-1)\bar{x}\bar{y}$$

and other variables are as previously defined. This expression for the variance of p is used as a starting point in estimating sample size. The square of the coefficient variation of p is given by $Cpp = v(p)/p^2 = 1/n\,[Cyy + Cxx - 2Cyx]$. The approximate sample size, n_o, may be estimated by specifying desired values for the coefficient of variation of p (cv(p)) and solving for n, i.e.

$$n_o = (C_{yy} + C_{xx} - 2C_{yx})/C_{pp}.$$

Specification of equal values for cv(p) for all values of p results in a narrowing of the half confidence interval, $|d|$, as p decreases. To obtain approximately equal confidence intervals throughout the range of p, the values of cv(p) were varied according to the value of p. This was done by grouping the values of p into class intervals (0-.10, .10-.20, ... , .90-1.00) and finding the value of cv(p), which gave the desired value of $|d|$ at the mid-point in each class interval, p_o, i.e. $|d| = 2$ (standard deviation of p), hence $|d| = 2cv(p_o)p_o$, or $cv(p_o) = |d|/2p_o$. Specification of values for $|d|$ of 0.05 and 0.10 gave the values of

TABLE III

Confidence limits for p and relevant data for estimating proportion of larch sawfly cocoons parasitized by *B. harveyi*

Source of data	Coefficients of variation		$C_{\bar{y}\bar{y}}$	$C_{\bar{x}\bar{x}}$	$C_{\bar{y}\bar{x}}$	95% Confidence limits for p			
						Student's t		Quadratic limits	
	$\bar{x}$	$\bar{y}$				Lower	Upper	Lower	Upper
Whiteshell, Group I, 1956	.162	.205	.0422	.0264	.0295	.1522	.2332	.1463	.2329
Whiteshell, Group I, 1957	.171	.244	.0594	.0292	.0386	.1699	.2707	.1534	.2692
Whiteshell, Group II, 1957	.142	.135	.0182	.0201	.0183	.2593	.3095	.2602	.3143
Whiteshell, Group III, 1957	.240	.285	.0810	.0574	.0644	.2903	.4549	.2540	.4532
Whiteshell, Group IV, 1957	.044	.048	.0023	.0019	.0016	.2612	.2896	.2673	.2931
Pierceland, 1955	.227	.725	.5259	.0515	.1043	0	.0331	0	.0317
Pierceland, 1956	.355	.501	.2512	.1260	.1610	.0621	.1899	0	.1984
Pierceland, 1957	.242	.293	.0861	.0587	.0649	.0766	.1917	.0661	.1987
The Pas, 1958	.252	.251	.0628	.0634	.0611	.4607	.6031	.4549	.6239
Cranberry Portage, 1958	.232	.204	.0418	.0536	.0338	.1683	.3483	.1804	.3946

$cv(p_o)$ shown in Table II. These values were used in the formula for estimating n_o.

The results indicate that 20 four-square-foot units should provide satisfactory estimates of the percentage *B. harveyi* parasitism over a wide range in sawfly populations (2.28 to 31.80 cocoons per square foot of collecting area) and *B. harveyi* parasitism (.014 to .532).

Confidence Limits

Cochran (1953) states that "the normal approximation applies reasonably well if the sample size is at least 30 and is large enough so that the cv's [coefficients of variation] of $\bar{y}$ and $\bar{x}$ are both less than 0.1." When these conditions are not met he suggests estimating approximate limits by use of the quadratic formula

$$p = \hat{p}\left\{\frac{(1 - t^2C_{\bar{y}\bar{x}}) \pm t\sqrt{(C_{\bar{y}\bar{y}} + C_{\bar{x}\bar{x}} - 2C_{\bar{y}\bar{x}}) - t^2(C_{\bar{y}\bar{y}}C_{\bar{x}\bar{x}} - C_{\bar{y}\bar{x}}^2)}}{1 - t^2C_{\bar{x}\bar{x}}}\right\}$$

where $\hat{p}$ is the value of p estimated from the sample; t is Student's t for the desired confidence level with n-1 degrees of freedom;

$$C_{\bar{y}\bar{y}} = C_{yy}/n;\ C_{\bar{x}\bar{x}} = C_{xx}/n;\ \text{and}\ C_{\bar{y}\bar{x}} = C_{yx}/n.$$

The cv's of $\bar{y}$ and $\bar{x}$ were calculated for each group of data (Table III), and with one exception (Whiteshell, Group IV, 1957) are all larger than 0.1. The confidence limits obtained by using Student's t in the conventional manner were therefore compared with the limits obtained by solving quadratic formula (Table III). The conventional limits are consistently narrower than the quadratic limits, but this difference in the widths of the limits is less than 3.5 per cent except for the 1956

Pierceland data. In this case the conventional limits indicate a significant increase in the percentage of *B. harveyi* parasitism, compared to 1955, but the quadratic limits suggest that this is not so. The calculations for obtaining the quadratic limits are lengthy in comparison to conventional methods, but are recommended on the basis of these results.

Summary

A technique is presented for estimating parasitism of larch sawfly cocoons by *B. harveyi* in survey collections. The cocoons are obtained from 4-square-foot moss filled trays placed under the tree crowns. The trays should be scattered throughout each plot, because of intra-plot variability in parasitism. Twenty trays per plot will provide satisfactory estimates of *B. harveyi* parasitism. Confidence limits for the proportion parasitized should be estimated by a quadratic approximation, and not by the conventional use of Student's t.

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(Received March 20, 1959)

Note on Occurrence and Nesting Habits of *Ancistrocerus waldenii waldenii* (Vier.) (Hymenoptera : Vespidae) in Newfoundland[1]

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On July 7, 1958, at Churchill Park, St. John's, a number of wasps were observed boring holes into the mortar between the bricks of a private dwelling. A total of 41 holes, three-sixteenths of an inch in diameter and up to three inches in depth, were counted. The majority of these holes faced south and a few faced west. Some were provisioned with small green caterpillars and capped, and others were in the process of excavation. This unusual nesting habit, and the presence of the wasps, caused much anxiety to the owner. One spraying with a five per cent DDT solution, concentrated in and around the holes, eliminated the infestation.

Mr. C. D. Miller (in litt.), Entomology Division, Ottawa, determined the species as *Ancistrocerus waldenii waldenii* (Vier.). Miller (1954) recorded a similar habit for *A. parietum* (L.) at Ottawa.

The following distribution of *A. waldenii waldenii* (Vier.) was given by Bequaert (1943): throughout the northern and central United States and southern Canada. The southern limit seems to run from northern California and northern New Mexico to Virginia. Northward it extends to southern Labrador and central Alaska (Mt. McKinley Nat. Pk., 63° N.), this being one of the two solitary vespids that range the farthest north in the New World. In describing its nesting habits, Bequaert stated that it was known to build mud-nests on walls or rocks.

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[1]Contribution No. 3911, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

(Received March 2, 1959)

Observations on the European Pine Sawfly, *Neodiprion sertifer* (Geoff.), and its Parasites in Southern Ontario[1]

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Introduction

The first North American collection of the European pine sawfly, *Neodiprion sertifer* (Geoff.), was made in Somerset County, New Jersey, in 1925 (Hamilton, 1943). It was first recorded in Canada near Windsor, Ontario, in 1939 (Raizenne, 1957), and by 1946 it had spread as far east as London (Watson, 1946). This serious pest of pines has continued to spread, and is now found throughout most of southwestern Ontario (Fig. 1) (Sippell and MacDonald, 1958). This is the only infestation of this species in Canada.

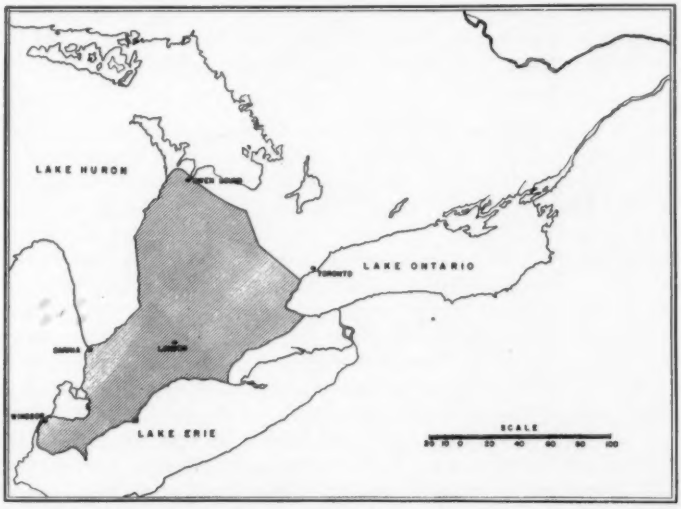

Fig. 1. Distribution of *Neodiprion sertifer* in southern Ontario, 1957. (Sippell and MacDonald, 1958).

There is an extensive European literature dealing with this species, but published reports on it from North America are few. Short descriptions of life stages and outlines of seasonal history and parasitism in the United States have been given by Schaffner (1939), Girth and McCoy (1946a, 1946b), and Craighead (1950). Hamilton (1943) has reported on chemical control, Brygider (1952) on overwintering of eggs, Holling (1955) on predation by small mammals, and Bird (1950, 1952, 1953, 1955) on control by a virus disease. A note by Finlayson and Finlayson (1958) lists 14 species of parasites obtained from cocoons in southwestern Ontario during five recent years.

The main part of this study was conducted in 1953 in the vicinity of Strathroy, Ontario, with some observations and collections being made in study plots near Muncey, Bothwell, Grand Bend, and Mount Brydges, all located within a 30-mile radius of Strathroy. Additional data on parasitism were obtained in 1954 and 1955 in the same plots. The bulk of the work was done in

[1]Contribution No. 550, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada.

plantations of Scots pine, *Pinus sylvestris* L., a species extensively planted for Christmas trees in southwestern Ontario. Oviposition studies were also made on two other host tree species, red pine, *P. resinosa* Ait., and jack pine, *P. banksiana* Lamb. Other recorded hosts of this species are Japanese red pine, *P. densiflora* S. and Z., and mugho pine, *P. mugo* Turra. (Schaffner 1939).

Biology

N. sertifer is univoltine. Eclosion commences in southern Ontario in the first half of May and continues for one to two weeks. The larvae are gregarious and eat only the old foliage. Feeding continues until the latter half of June, when the fully-developed larvae drop to the ground and spin cocoons in the duff. Adults emerge and oviposit from early September until late in the autumn. The eggs are laid in slits cut in the edges of the current year's needles, each needle receiving a row of from two to eight more or less uniformly spaced slits. A number of needles are utilized for oviposition on a single shoot, and since these needles are confined to a limited portion of the shoot, usually at or near the tip, eggs on a single shoot may justifiably be referred to as an "egg cluster". A single cluster is thought to include the total egg complement of one female.

The Egg

Studies of egg clusters on 1952 foliage indicated that those on Scots pine at Strathroy averaged 87.0 $\pm$ 7.64 eggs per cluster, while clusters on jack pine at Muncey averaged 76.8 $\pm$ 4.12, and on red pine at Mount Brydges, 80.2 $\pm$ 8.51. These means, each based on samples of 20 clusters, do not differ significantly in the appropriate "t" tests. Egg cluster size was, therefore, similar to that obtained for other southwestern Ontario populations by Rose (1952), but lower than that reported by Schwerdtfeger (1936) in Europe, who found clusters of from 49 to 231 eggs, with an average of 118. Hamilton (1943) indicated that the larger clusters in New Jersey contained "200 or more" eggs, but did not give an estimate of average size.

The mean number of eggs per egg-bearing needle on both Scots and jack pine was 4.8 $\pm$ 0.05, but on the longer-needled red pine it was 7.2 $\pm$ 0.18. In 66 per cent of the egg-bearing needle pairs examined, eggs were laid in only one of the needles. When eggs were found in both needles of a pair, they occurred with equal frequency in adjacent and opposite edges. Less than one per cent of the needles examined bore eggs on both edges.

Hatching success was greater on Scots than on either jack or red pine, for which values were similar. The majority of unhatched eggs on all host species

TABLE I.

Hatching of eggs laid on three tree species

Host Tree	No. Eggs Examined	Per cent Hatch[1]	Contents of Unhatched Eggs	
			Per cent Eggs Containing Dead Larvae	Per cent Undeveloped Eggs
Scots pine	1740	95.0	1.2	3.8
jack pine	1537	90.7	2.1	7.2
red pine	1524	88.1	2.3	9.6

[1]Differences in hatch statistically significant (2 x 2 contingency test) only between Scots and jack and Scots and red pines. No other differences are statistically significant.

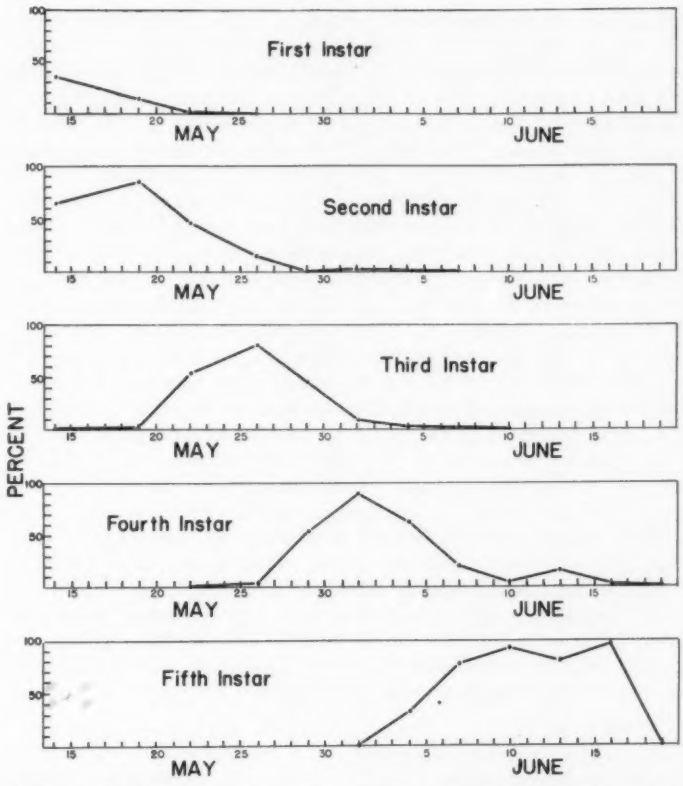

Fig. 2. Larval development on Scots pine, Bothwell, Ont. 1953. Based on collections of approximately 400 larvae made every third day throughout the larval period.

failed to develop to a recognizable larval form (Table I). Similar results have been reported by European workers, Schwerdtfeger (1936) reporting egg mortality of less than five per cent in Poland, and Thalenhorst (1952) mortalities of six and five per cent in two areas in northern Germany, both for eggs laid on Scots pine.

Larval Stages

Immediately after eclosion, the first-instar larvae commence feeding in groups on the egg-bearing needles. In this stage they do not consume the whole needle, but merely skeletonize it, avoiding those portions in which the egg slits were cut. The partially eaten needles soon wither and curl, giving a characteristic appearance to the twig. The later instars also feed gregariously, but consume whole needles. Male larvae pass through four and female larvae through five feeding stages before moulting to prepupae. The term *prespinning larvae* has been adopted for the active, motile prepupae during the period from the final larval moult until the insect has become immobile within its cocoon. This "stage" is easily identified by changes in larval coloration marked by the breaking up of the dorsal longitudinal stripe, by the generally less distinct colour differences between stripes and ground colour, and by the change in

head capsule coloration from black to brown. The prespinning larvae do not feed, but drop to the ground and, after some wandering, spin cocoons.

The progress of larval development is illustrated in Fig. 2. Although there is considerable overlap in the development of successive instars, as many as 80 or 90 per cent of the larvae reach a common instar by the time the moult to the next instar begins. This regular development seems to be characteristic of pine sawflies that overwinter as eggs such as *N. sertifer* and *N. pratti banksianae* Roh. (unpublished data), and is in contrast to a markedly greater spread in development of pine sawflies that overwinter in the cocoon, such as *N. lecontei* (Fitch) on red pine (unpublished data). These differences are probably related to a greater variability in soil and duff temperatures compared to air temperatures from place to place in the early spring.

Larval mortality under field conditions was studied by following the development of larvae on two lightly-infested, open-growing Scots pine trees, under which trays had been placed to catch falling larvae. The trays, which were slightly larger than the crown projection of the trees, consisted of rectangular wooden frames with factory cotton bottoms through which the bole of the tree projected. The sides of the trays were coated with "tanglefoot".

Fourteen clusters of first-instar larvae were found on the two trees under observation. Direct counts of egg number and hatching success could not be made without unduly disturbing and dispersing the first-stage larvae, so that in the calculations that follow the initial populations were calculated using data on egg numbers and hatching success. The first direct counts were made on May 22, when the population consisted of approximately equal numbers of second-and third-instar larvae. Twice-weekly examinations of the trays were made throughout the larval period. From this study the following estimate of loss during the feeding stages has been made:

Egg population:		
14 clusters assumed to average 87.0 eggs per cluster	14×87.0	$= 1218$
Emerged larvae:		
1218 eggs assumed to average 95.0% hatching success (Table I)	$1218 \times .950$	$= 1157$
Initial census:		
Direct count II and III-instar larvae, May 22		895
Calculated loss during early larval development		262, or 22.6% of 1157
Larvae completing development:		
Last feeding stage and prespinning larvae found on trays, June 4 to 18		875
Loss during late larval feeding stages		20, or 1.7% of 1157
Total loss, feeding stages		24.3%

It is apparent from the foregoing that little mortality occurred among feeding larvae once they had reached the second and third instar. The data further suggest appreciable mortality during the early larval stages. Ghent (1954) has demonstrated that in laboratory rearings of *N. pratti banksianae* the heaviest mortality occurs during the first instar, and is attributable to the failure

TABLE II.

Analysis of cocoons in two permanent sample plots.

Mt. Brydges

Category	1953		1954	
	No. per sq. ft.	per cent	No. per sq. ft.	per cent
Sound	25.8	12.7	12.4	6.2
Dead sawfly	21.2	10.4	22.0	11.1
Cocoons with holes				
Adult sawfly emerged	58.0	28.5	52.1	26.4
Opened by small mammals	35.9	17.7	26.1	13.2
Other holes	62.4	30.7	85.4	43.1
Total	203.3	100.0	198.0	100.0

Strathroy

Category	1953		1954	
	No. per sq. ft.	per cent	No. per sq. ft.	per cent
Sound	13.2	5.8	3.0	1.4
Dead sawfly	8.9	4.0	6.6	3.2
Cocoons with holes				
Adult sawfly emerged	54.3	24.1	51.2	25.2
Opened by small mammals	34.7	15.3	24.9	12.3
Other holes	114.9	50.8	117.6	57.9
Total	226.0	100.0	203.3	100.0

of the newly-hatched larvae to establish and maintain themselves as feeding insects on mature jack pine foliage. Larvae reared in groups profit from sharing feeding incisions in the needles, and it is to this that Ghent attributes the selective advantage that has brought about the evolution of the group-feeding behaviourism. It is probable that the mortality of *N. sertifer* occurring before the census of May 22 reflects this same difficulty in becoming established on the mature needles of Scots pine.

Of the 895 second-and third-instar larvae present on May 22, only 20 failed to complete larval development. Of these, eight dropped to the trays as third-instar larvae, leaving a loss of only 12 larvae to be attributed to bird, insect, or other predation — a figure that suggests that predation during the larval stages was not an important mortality factor.

Many larvae do not moult to the prespinning stage until they have dropped to the ground. Of the 875 fully developed larvae found on the trays, only 554, or 63.3 per cent, were prespinning larvae, and some of these may have dropped as last feeding-stage larvae, and moulted on the trays between examinations. But the remainder of the larvae, 321 or 36.7 per cent, were found as fully-developed last feeding-stage larvae, so that these provide a minimum estimate of the proportion of this population that dropped *before* moulting to prepupae.

Cocoon

This phase of development was studied through cocoon collections made in two plantations, each collection consisting of 150 one-square-foot quadrats. Sampling was done in late August and was restricted to areas beneath the tree crowns. Prebble (1943), working with the European spruce sawfly, found that such a restriction greatly reduced sampling variability. The results of analysis of these collections are shown in Table II. No distinction was made between cocoons spun in previous years and those spun in the current year.

In examining cocoon samples, cocoons could be separated into a number of categories, as indicated in Table II. *Sound* cocoons were those containing living insects, including those that had been parasitized. Cocoons categorized as *dead sawfly* consisted of all unopened cocoons in which the sawfly had died from unknown causes. As the collections were made before the current adult emergence, the *adult sawfly emerged* category comprised only cocoons from which adults had emerged in previous years. Cocoons in the *opened by small mammals* class were separable from other opened cocoons by the type of hole in them. The jagged, asymmetrical holes chewed by small mammals can be readily distinguished from the smooth uniform holes made by emerging sawflies and by parasites and other predators (Holling 1955). Cocoons under *other holes* included all those with emergence holes made by parasites and those attacked by non-mammalian predators. Also included in this category was the small proportion of opened cocoons that had deteriorated to such a point that accurate classification was impossible. These generally constituted only one or two per cent, and never over five per cent, of the cocoon population.

Individual yearly samples in Table II, each consisting of approximately 30,000 cocoons, represent the sort of cross-section of a population's history that may be obtained through cocoon sampling. Caution must, however, be exercised in drawing conclusions about the particular populations represented by these data, since information is given for only two consecutive years at a time when the population was declining. The small numbers in the *sound cocoons* category, on which the continued existence of the population depends, is striking when it is considered that this category contained developing parasites as well as living prepupae. A decline in the proportion of sound cocoons from 1953 to 1954, indicative of the continuing action of virus disease introduced into these plantations in 1950 (Bird 1953), is seen in both plantations. The large number of cocoons in the *other holes* category indicates that parasitism and non-mammalian predation were the most important factors operating against cocooned larvae in these plots. Small mammal predation was solely the work of *Peromyscus maniculatus bairdii* Hoy and Kennicott, the only species found in these small plantations. In larger plantations several species of small mammals including such highly efficient predators as the shrews, are regularly present (personal communication, C. S. Holling), so that the mortality attributable to small mammal predation there would constitute a higher proportion of total mortality than was found in these plots.

The sex ratio of sound cocoons in the two plots immediately after spin-up in mid-June, and again in late August, is given in Table III. The preponderance of males at Mt. Brydges and Strathroy immediately after spin-up may be attributable to the presence of virus disease in these populations, since female larvae may suffer greater mortality from virus because they are exposed to it for one more feeding instar. In populations that are free of virus, females are more numerous than males, as indicated by the 1952 collection at Bothwell. The slight reduction in proportion of females from mid-June to late August in 1952

TABLE III.

Sex ratios based on cocoon collections

Year	Plot	Mid-June				Late August			
		No. of Cocoons		Sex Ratio		No. of Cocoons		Sex Ratio	
		♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
1952	Bothwell	1365	2047	1	1.5	199	244	1	1.2
	Mt. Brydges	3820	3445	1	0.9	715	62/	1	0.9
	Strathroy	1551	1280	1	0.8	872	583	1	0.7
19 3	Mt. Brydges	1155	896	1	0.8	832	60	1	0.7
	Strathroy	1903	1086	1	0.6	678	3	1	0.5

and 1953 can be attributed to the action of small mammals, which tend to open more female than male cocoons (Holling 1954), a tendency that might markedly affect the sex ratio at high predation levels.

Adult

Emergence time of adults and the incidence of overwintering in the cocoon were based on daily examinations of cocoon collections kept under natural conditions. First female adult emergence was recorded on September 5 and first male adult emergence on September 7, 1953. Emergence of both sexes continued through to the last regular field examination on October 8, as illustrated in Fig. 3. Cocoons remaining after October 8 were again examined on December 15, 1953, at which time considerable additional emergence was recorded. 44.3 per cent of the total 1953 adult emergence took place after the last of the daily examinations on October 8. Thus, an appreciable part of the adult emergence of this species may be expected to take place in the late autumn.

Comparison of the emergence-histograms in Fig. 3 suggests that males and females responded in the same way to whatever conditions made a day one of heavy or light emergence (Coefficient of correlation 0.82, $p<0.001$). This synchrony in emergence greatly increases the probability of mating. Its existence is remarkable in that the majority of male larvae cease feeding and drop to the ground four to five days before the females.

All individuals of this species do not reach the adult stage in one season. Of 5,614 sound cocoons collected at Bothwell in the summer of 1952 and placed in emergence boxes in the ground, where they were protected from small mammal predation, 1,369, or 24.4 per cent, produced adults the same year, after about three months in the cocoon. Another 431, or 7.7 per cent, produced adults the following year, after approximately 15 months in the cocoon. Of 1,950 overwintered cocoons collected at Mt. Brydges in the spring of 1952, 58 or 3.0 per cent did not emerge until the autumn of 1953, after some 27 months had been spent in the cocoon. The survival of cocooned larvae through one or more overwintering periods in the field must serve to buffer a population against the catastrophic elimination of a single year-class.

The overwintering of prepupae of this species has also been reported in England by Robbins (1931) and in Belgium by Elens (1953), but Thalenhorst (1952) failed to find any such overwintering in northern Germany. Emergence of adults in the spring from overwintering residue populations, which has been

reported from continental Europe by Shiperovich (1952), did not occur in Ontario.

Parasites

Parasite Species

The following species of parasites were obtained from *N. sertifer* in this study:

Diptera
- Bombyliidae
  - *Hemipenthes sinuosa* (Wd.)
- Muscidae
  - **Muscina stabulans* (Fall.)
- Phoridae
  - **Megaselia* sp.

Hymenoptera
- Eulophidae
  - *Dahlbominus fuliginosus* (Nees)
  - **Tetrastichus* sp.
- Pteromalidae
  - **Tritneptis klugii* (Ratz.)
- Braconidae
  - **Aspilota* sp.
- Ichneumonidae
  - *Aptesis indistincta* (Prov.)
  - *Delomerista diprionis* (Cush.)
  - *Endasys subclavatus* (Say)
  - *Euceros frigidus* Cress.
  - *Exenterus canadensis* Prov.
  - **Mastrus aciculatus* (Prov.)
  - *Mastrus argeae* (Vier.)

The six species marked with asterisks in the above list have not previously been reported from *N. sertifer*. The remaining eight were previously recorded from *N. sertifer* from southern Ontario by Finlayson and Finlayson (1958). So far as is known, this is the first record of *Muscina stabulans* as a parasite of a sawfly, but all others listed above have been recovered from native species (Daviault 1943; Townes and Townes 1951; Brooks 1952; and Forest Insect Survey Records, Sault Ste. Marie).

In addition to the above species, the following have been obtained from *N. sertifer* in southwestern Ontario: *Agrothereutes* sp., *Aptesis basizonia* (Grav.), *Eupelmella vesicularis* (Retz.), *Exenterus abruptorius* (Thumb.), *Diplotichus hamatus* (A. and W.), and *Spathimeigenia erecta* Ald. (Finlayson and Finlayson, 1958); and *Exenterus amictorius* Panz., *Dibrachys cavus* (Wlkr.), *Neophorocera claripennis* (Macq.) and *Neophorocera* sp. (Raizenne, 1957).

Host stage attacked

There was no parasitism of the *N. sertifer* eggs examined in the spring of 1953, nor of some 70,000 eggs collected and reared through the larval period at the Laboratory of Insect Pathology, Sault Ste. Marie, in 1950, 1951, and 1952. Furthermore, no parasites were obtained by rearing some 2500 feeding stage larvae collected in lots of approximately 300 at three-day intervals throughout the larval feeding period. All the parasites were reared from cocooned prepupae collected as cocoons, with the exception of *Exenterus canadensis*, which was recovered from cocooned prepupae reared from field-collected prespinning

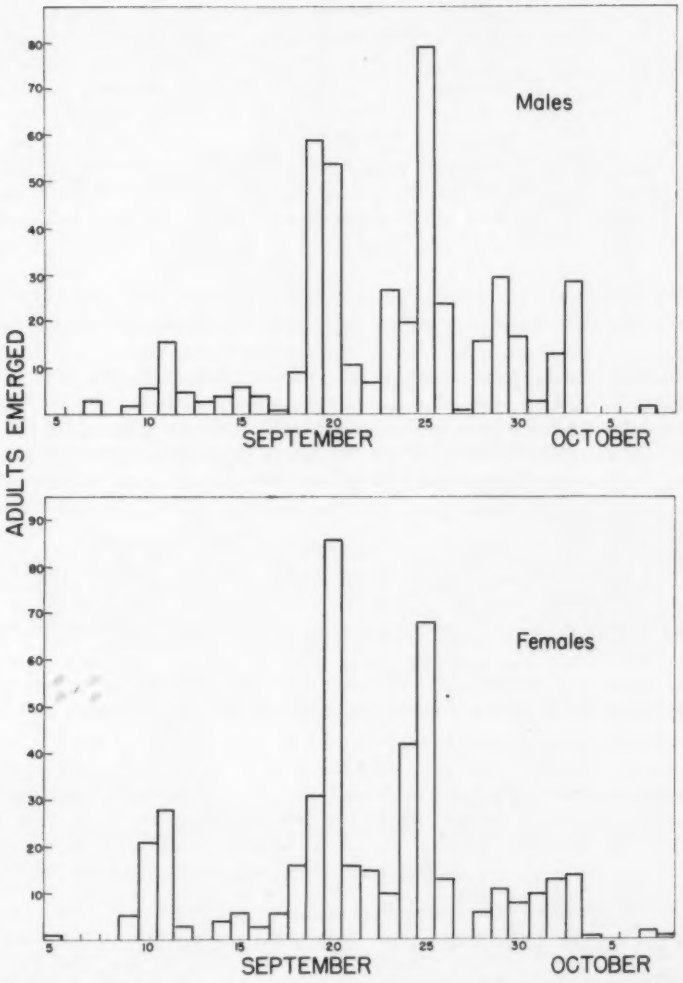

Fig. 3. Numbers of adult sawflies emerged throughout field season, Strathroy, Ont., 1953.

larvae. It would thus appear that none of the parasites recovered parasitize the feeding stage larvae; *Euceros frigidus* is, however, known to parasitize feeding larvae of *N. pratti banksianae* (unpublished data).

Adult emergence

With the exception of the multivoltine *Dahlbominus fuliginosus* all parasites overwintered within the host cocoon and emerged as adults during the year following attack. Depending on whether attack by *D. fuliginosus* was by adults of an early or late summer generation new adults of this species emerged during the year of attack or the year following attack. It would be reasonable to expect that the other chalcidoids recovered in this study, *Tetrastichus* sp. and *Tritneptis klugii* might also emerge during the season of original attack, but

TABLE IV.
Parasitism.

Year	Mt. Brydges			Strathroy		
	No. sq. ft. Sampled	Sound Cocoons per sq. ft.	Per cent Para.	No. sq. ft. Sampled	Sound Cocoons per sq. ft.	Per cent Para.
1953	148	25.8	18.2	150	13.2	29.1
1954	150	12.4	8.9	150	3.0	16.6
1955	149	6.2	11.1	147	3.1	8.1

in the limited numbers occurring in these collections, this was not observed. Small numbers of two species, *Exenterus canadensis* and *Hemipenthes sinuosa*, overwintered a second winter in the host cocoon and emerged during the second year after attack. Most of the Hymenoptera emerged in June, the remainder in July and August; the Diptera all emerged in late July and early August.

Degree of parasitism

Because all the parasites recovered emerged from the host cocoon, it was possible to determine the degree of parasitism and the relative abundance of species by sampling cocoons. Parasitism, expressed as a percentage of sound (i.e. healthy plus parasitized) prepupae, is given for two populations during three years in Table IV.

The relative abundance of the more common parasite species in all areas sampled, based on intensive cocoon samples in the Strathroy and Mt. Brydges

TABLE V.
Relative abundance of parasites in cocoon collections, expressed as per cent of total parasites recovered from sample

Species	Mt. Brydges			Strathroy			Bothwell		Grand Bend	Bay-field
	1952	1953	1954	1952	1953	1954	1952	1954	1954	1955
Hemipenthes sinuosa	55.8	50.0	53.3	28.4	21.3	33.3	2.6	6.3	7.1	10.5
Dahlbominus fuliginosus	3.3	2.4	13.3	3.4	3.8	5.6	0.6	6.2	3.6	3.7
Tritneptis klugii	0	2.0	3.4	0	0	0	0	0	0	0
Aptesis indistincta	0	0	0	0	0	0	6.1	0	3.6	0
Delomerista diprionis	0.5	0	0	0	0	22.1	0	0	0	0
Endasys subclavatus	3.3	7.6	13.3	27.5	17.9	16.7	16.7	0	10.8	6.8
Euceros frigidus	12.7	19.0	0	16.2	40.1	16.7	34.5	25.0	7.1	4.2
Exenterus canadensis	24.4	19.0	16.7	24.5	16.9	5.6	32.8	62.5	60.7	72.7
Mastrus aciculatus	0	0	0	0	0	0	6.7	0	0	0
Mastrus argeae	0	0	0	0	0	0	0	0	7.1	2.1

areas and on general cocoon collections in the remaining areas, is shown in Table V. The degree of parasitism varied considerably between the two areas sampled and between years (Table IV), although the parasite complex was generally constant both between areas and years (Table V).

Discussion

The seasonal history of *N. sertifer* in southwestern Ontario appears to be very similar to that described for both the United States and Europe, although differences are recorded by European workers on the overwintering of cocoons and the emergence of adults from them in the spring. Size of egg clusters (on Scots pine) appear to be smaller in Ontario than reported for either the United States or Europe, with hatching success being similar to that in Europe.

The major difference in parasitism between Ontario and Europe is the absence of egg parasites in Ontario; in Europe eggs are at times quite heavily parasitized by chalcids (Baer, 1916) and are also attacked by proctotrupoids (Shiperovich, 1927; Sturm, 1942). No mention is made by European authors of parasitism of feeding stage larvae, but reference is made to *Exenterus* spp. parasitizing prespinning larvae (Robbins, 1931; Kangas, 1941; Thalenhorst, 1952) in a manner similar to that by *E. canadensis* in Ontario.

As in Ontario, cocooned prepupae are parasitized to a variable extent in Europe, although total parasitism reported for European populations is generally higher than that found in Ontario. In Austria, Schonwiese (1934) reported 49 and 89 per cent parasitism in 1931 and 1932, whereas in north Germany, Thalenhorst (1952) reported parasitism of 33, 38, and 55 per cent in three different plots in 1949. Total parasitism in two plots in Ontario during the three years 1953-1955 ranged from 8.1 to 29.1 per cent of sound cocoons.

Acknowledgments

The author is greatly indebted to Dr. F. T. Bird, Laboratory of Insect Pathology, Sault Ste. Marie, for permission to use data collected by him before 1952. Thanks must also be given to several colleagues and especially to A. W. Ghent, for invaluable assistance in the preparation of the manuscript, and to the officers of the Insect Systematics Unit, Science Service, Department of Agriculture who identified the parasites obtained.

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(Received April 23, 1959)

A Technique for Estimating Tamarack Foliage Production, A Basis for Detailed Population Studies of the Larch Sawfly[1]

By W. G. H. Ives[2]

This paper is one in a series on sampling techniques used in population studies of the larch sawfly (Ives, 1955; Ives and Prentice, 1958). The technique has been developed to provide bases for comparing the intensity of sawfly infestations in stands of different compositions, and for studying the effect of the insect upon its host. A preliminary study demonstrated the feasibility of developing a sampling method for estimating foliage weight, but also indicated that the foliage weight increased as the season progressed (Ives, 1958). Foliage sampling in stands infested by the larch sawfly must be completed before defoliation becomes prevalent, and the foliage weight may increase considerably after sampling. In 1956 an intensive sampling program was carried out on tamarack in the Whiteshell Forest Reserve, Manitoba, to determine the sample size needed to obtain statistically acceptable estimates of foliage production and to study the nature of changes in foliage weight during the season.

Foliage Sampling

Two plots measuring one-half by three chains were located in stands of pure tamarack. Plot I contained 61 trees having an average height of 33 feet and an average d.b.h. of 4.5 inches. The plot was very wet, with a large portion of the forest floor still covered by surface water at the end of the sampling period (July 10). So far as is known, the plot had not been affected by sawfly attack during the previous 10 years (Nairn, 1958). Plot II contained 59 trees having an average height of 38 feet and an average d.b.h. of 5.0 inches. It was moderately dry, and had been subjected to sawfly attack for several years. The undergrowth in both plots consisted primarily of alder. The dominant ground cover was mosses and sedges in Plot I and mosses and Labrador tea in Plot II.

The heights of the trees were measured with a Haga altimeter. The height above ground of the lowest portion of the crown was measured with a pole and marked off as a "measuring-stick" and subtracted from the tree's height to provide the crown depth for each tree. Each crown depth was divided into three equal levels and the number of branches in each level counted with the aid of binoculars soon after the buds had burst. The diameters of the trees at breast height were measured and the crown forms classified into four categories: high; slender; irregular; and full.[3] Three increment borings were removed from each tree and the amount of the previous year's growth measured.

Pole pruners were used to remove two randomly selected branches from each crown level. This sampling was conducted during a two-week period commencing June 25, approximately one week after linear foliage growth had apparently stopped. The branches were placed in individual cloth bags and hung in a warm place to dry. The dry foliage was removed from the branches, sifted to remove bark scales, spurs, and other litter, and placed in seamless metal boxes. After drying for 48 hours at 105 degrees Centigrade, the foliage was weighed to the nearest 0.1 gram.

Bases for stratification

Previous work has shown that the number of branches differs between crown levels (Ives, 1955) and similar results were obtained in this study. The

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[3]These crown form classifications will be described in a paper to be published shortly by L. D. Nairn and R. M. Prentice, Forest Biology Laboratory, Winnipeg, Manitoba.

TABLE I.

Analyses of variance for testing tree and crown level effects on the weight of foliage per branch.

Source	Plot I		Plot II	
	Degrees of freedom	Mean square[4]	Degrees of freedom	Mean square
Trees	60	321.48*	58	421.70**
Crown levels	2	2105.12**	2	1348.77**
Interaction	120	199.97	116	276.98**
Error	183	205.36	177	196.96

[4]Throughout this paper a single asterisk indicates significance at the .05 level and a double asterisk indicates significance at the .01 level.

objective of the following analyses is to determine which factors affect the variability in foliage weight per branch and foliage weight per tree.

Foliage weight per branch–The amount of foliage per branch differed between crown levels and between trees on both plots (Table I) but the presence of interaction on Plot II shows that the differences were not consistent. This is probably a result of continued defoliation, which varies in intensity between trees.

It is concluded that stratification by crown levels increases the accuracy of estimates of tamarack foliage production.

Foliage weight per tree–The estimate of the mean foliage weight per tree was obtained from the formula

$$F = \frac{1}{n} \sum_{i=1}^{n} \sum_{j=1}^{3} y_{ij} x_{ij\cdot}$$

where n is the number of trees in the sample, y_{ij} is the number of branches in the j^{th} crown level of the i^{th} tree (assumed to be without error),
and

$$x_{ij\cdot} = \frac{1}{2} \sum_{k=1}^{2} x_{ijk}$$

is the observed mean weight of foliage per branch in the j^{th} crown level of the i^{th} tree.

TABLE II

Summary of analyses of variance tests conducted with estimated weight of foliage per tree to determine bases for stratification of sample.

Factor	Plot I			Plot II		
	Degrees of freedom		F	Degrees of freedom		F
	n_1	n_2		n_1	n_2	
Height	1	59	3.12	1	57	0.43
Crown depth	1	59	6.68*	1	57	16.03**
d.b.h.	1	59	8.89**	1	57	13.35**
Estimated increment	1	59	13.77**	1	57	15.59**
Crown class	3	57	5.13**	3	55	4.30**

TABLE III.

Estimated weight of foliage per tree (in grams) for different classes of trees.

Tree classification[6]	Plot I		Plot II	
	Number of trees	Foliage weight	Number of trees	Foliage weight
H < 30 < 23 < 5	0	—	2	294
H ⩾ 30 < 23 ⩾ 5	0	—	1	1742
H < 30 ⩾ 23 < 5	0	—	1	225
H ⩾ 30 ⩾ 23 < 5	2	804	1	890
H < 30 ⩾ 23 ⩾ 5	0	—	1	1030
S < 30 < 23 < 5	3	345	6	378
S < 30 ⩾ 23 < 5	2	646	0	—
S ⩾ 30 ⩾ 23 < 5	1	712	0	—
S < 30 ⩾ 23 ⩾ 5	0	—	1	990
S ⩾ 30 ⩾ 23 ⩾ 5	1	1252	2	1146
I < 30 < 23 < 5	12	714	12	515
I ⩾ 30 < 23 < 5	7	1206	2	598
I < 30 < 23 ⩾ 5	0	—	1	617
I ⩾ 30 < 23 ⩾ 5	1	652	6	787
I < 30 ⩾ 23 < 5	2	1218	4	886
I ⩾ 30 ⩾ 23 < 5	11	1091	4	871
I ⩾ 30 ⩾ 23 ⩾ 5	5	1234	4	1798
F < 30 < 23 < 5	2	495	1	1424
F ⩾ 30 < 23 < 5	1	1793	1	817
F < 30 < 23 ⩾ 5	1	676	1	704
F ⩾ 30 < 23 ⩾ 5	1	1810	1	998
F ⩾ 30 ⩾ 23 < 5	3	1792	3	2354
F ⩾ 30 ⩾ 23 ⩾ 5	6	2207	4	1562
Mean		1115		919

[6]The letters in the first column refer to the crown classifications, high, slender, irregular and full; the second column is the estimated stem increment in cubic inches; the third column is the crown depth in feet; and the last column is the d.b.h. in inches.

These estimates were used in analyses to determine which tree characteristics might be used for stratification of the sample. The factors considered were: tree height; crown depth; d.b.h.; crown class; and estimated 1955 increment in stem volume. The effects of the factors were determined from separate analyses of variance. The mean square for each factor was compared with the error for the respective analysis. This test procedure is probably rather insensitive, but does not utilize any assumptions about interactions between factors. The calculated F values show that crown depth, d.b.h., crown class, and estimated increment all provide bases for stratification of the sample (Table II).

Estimated weight of foliage per tree

The mean weights of foliage per tree for strata based on the above results are shown in Table III. The efficiency of stratification with proportional allocation was tested by an analysis of variance as shown in Table IV. An approximate estimate of the variance of the mean weight of foliage per tree is provided by the "Mean square" for "Within strata" divided by the number of trees (Cochran, 1953). Comparison of this estimated variance with that for simple random sampling shows that stratification reduced the variance by 25 and 32 per cent for Plots I and II respectively. The standard errors of the mean and the 95 per cent confidence intervals for the mean weight of foliage per tree using random and stratified sampling are presented in Table V. Stratification resulted in a reduction of the standard error by 14 per cent on Plot I and 17 per cent on Plot II. The estimated sample sizes required for a given degree of

TABLE IV.

Analysis of variance tables for testing effect of stratification in reducing variation in estimated weight of foliage per tree.

Source of variation	Degrees of freedom	Sums of squares	Mean square
Plot I			
Between strata	16	14971950	935747*
Within strata	44	18203107	413707
Total	60	33175057	
Plot II			
Between strata	20	17459029	872951*
Within strata	38	14113904	371418
Total	58	31572933	

accuracy are given in Table VI. These sample sizes are based on the mean weight of foliage per tree, utilizing the relation $d < s_{\bar{x}} t_\alpha$, which gives $n_o = s^2 t^2_\alpha / d^2$, where d is the half confidence interval width, $s_{\bar{x}} = s/\sqrt{n}$ is the standard error of the mean, and t_α is Student's t for the α confidence level, based on infinite degrees of freedom. The calculations assume the use of the same sampling procedure as used in this experiment.

It is concluded from these analyses that the increase in efficiency justifies the use of stratified sampling for estimating tamarack foliage production. A sample consisting of six branches from each of 30 trees should provide a satisfactory estimate of the amount of foliage per tree. Larger samples would be desirable, but the amount of work would be prohibitive if several plots were to be sampled.

Changes in Foliage Weight

Two bogs were chosen, one containing apparently healthy trees (Plot III), the other apparently stagnated ones (Plot IV). Three accessible branches were selected on each of five trees in each bog. The spurs of twelve uniform fascicles on each branch were marked with red aircraft dope. One randomly selected fascicle was removed from each branch at weekly intervals, commencing one week after linear foliage growth had apparently stopped. The fascicles were placed in individual vials and stored in a desiccating cabinet until dry. The needles were then removed from the spurs and the foliage dried in an oven at 105 degrees Centigrade for 48 hours before weighing (to the nearest 0.2 milligram).

TABLE V.

Standard errors and confidence intervals for mean weight of foliage per tree using simple random sampling and stratified sampling with proportional allocation.

Type of sampling	Plot I		Plot II	
	Standard error	95% confidence interval	Standard error	95% confidence interval
Random	95.76	$923 < \mu < 1307$	96.05	$727 < \mu < 1111$
Stratified	82.35	$949 < \mu < 1281$	79.34	$759 < \mu < 1079$

TABLE VI.

Approximate sample sizes needed to estimate mean weight of foliage per tree with various degrees of accuracy, using simple random sampling and stratified sampling with proportional allocation.

Confidence level	Plot I			Plot II		
	|d|[6]	Random sampling	Stratified sampling	|d|[6]	Random sampling	Stratified sampling
.95	112	171	128	92	248	169
.90	167	54	40	138	78	53
.90	223	30	23	184	44	30
.80	279	12	9	230	17	12
.80	334	8	6	276	12	8

[6]The size of the half confidence interval width based on 10, 15, 20, 25, and 30 per cent of the observed means for Plots I and II respectively.

The data from the weekly samplings were tested by analysis of variance, considering the 15 branches on each plot as blocks. The combined analysis of the two plots (Table VII) indicates highly significant plot and date of sampling differences with no interaction. The means for each sampling date were adjusted to eliminate plot differences by subtracting 1.35 (one-half the mean plot difference) from each mean in Plot III and by adding the same amount to each mean in Plot IV. The adjusted means for each sampling date are plotted against time in Fig. 1. The trends for both plots are similar and show a linear increase in foliage weight as the season progresses. The validity of using a common regression coefficient was tested by the errors of estimate technique (Snedecor, 1946). The F value obtained was 1.04 with 1 and 356 degrees of freedom, so that the use of an average regression is valid.

Considering the sampling date in terms of weeks (X) since linear needle growth had apparently ceased, the adjusted weight of foliage per fascicle (Y) may be estimated by

$$Y = 27.43 + 0.53X.$$

This formula is not meant to estimate the mean weight of foliage per fascicle at any given date, because the fascicles used in its calculation were not selected at random. However, the formula is useful for obtaining figures from which to calculate the percentage increase in foliage weight. For example, the estimated weight per fascicle increased 6.4 milligrams during the 12 weeks of sampling, which is an increase of 23.2 per cent over the estimated initial weight of 27.4 milligrams.

TABLE VII.

Combined analysis of variance for testing plot and date effect on foliage weight per fascicle.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F
Plot	1	652.86	652.860	16.20**
Date	11	1456.03	132.366	3.28**
Interaction	11	233.63	21.239	0.53
Blocks (pooled)	28	20873.41	—	
Error (pooled)	308	12413.87	40.305	

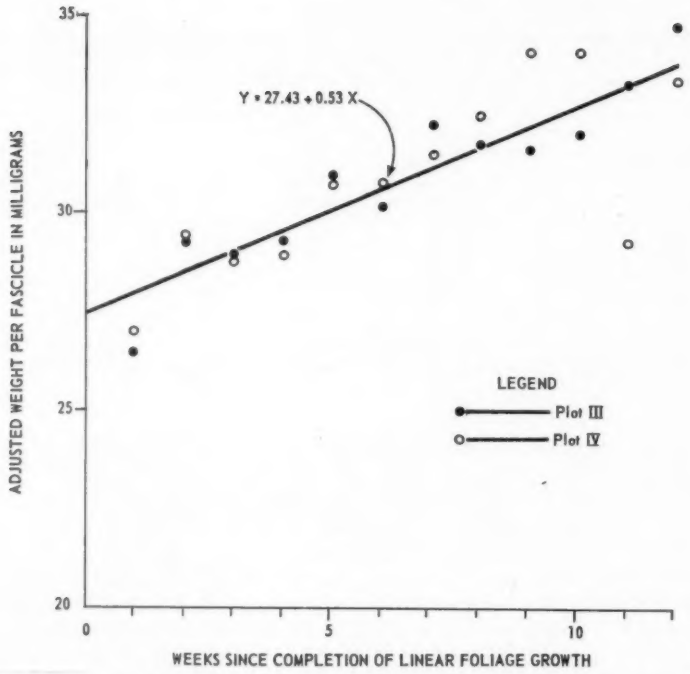

Figure 1. Adjusted foliage weight per fascicle and weeks since apparent completion of linear foliage growth. (See text for explanation of adjustment).

Discussion

A method has been presented for estimating tamarack foliage production. The method, of necessity, includes only branches that are large enough to be removed with pole pruners. It is difficult to establish size limits below which sampling is impossible, but if a shoot has side branches it is usually large enough to be sampled, and this was the criterion used during branch counting to determine what constituted a branch. Foliage production on branches under 12 inches in length may amount to as much as 60 per cent of the total in extreme cases of tree injury, but no figures are given to indicate the prevalence of trees in this extreme category (Nairn, 1958). Field observations by the present author indicate that it is usually small, unless the stand is deteriorating from prolonged sawfly attack or from flooding. Small branches arising from adventitious shoots occur on many trees that have been injured, but both their numbers and relative importance decrease on trees with fuller crowns. Furthermore, the error in estimates of foliage production on trees with very slender crowns would be much less than 60 per cent because many of the branches under 12 inches in length would be included in the branch counts and foliage sampling. The error introduced into foliage estimates by inability to sample small branches therefore is considered to be small for any trees that are not near death.

An important source of bias that must be guarded against is the tendency of field workers to consistently sample the largest branches. The bias was

overcome in this study by strict adherence to the randomly designated sampling points. The sample would otherwise seriously overestimate foliage production.

Analysis of the data has indicated that branches should be sampled from all crown levels, because the amount of foliage per branch differs for each level. Stratification of the sample on the bases of crown depth, d.b.h., crown class, and estimated increment in stem volume reduces the variation in estimated weight of foliage per tree. However, this categorization results in too many strata to be practical. It is suggested that stratification by crown depth and crown class should usually be adequate in homogeneous stands. In stands of mixed diameter classes additional stratification on the basis of d.b.h. or estimated increase in stem volume probably is desirable.

The increase in foliage weight during 12 weeks after linear needle growth had apparently ceased was 23 per cent of the original weight. An increase of this magnitude affects a foliage sampling program in a number of ways:

1. The increase in foliage weight may be accompanied by a change in nutritive value to the larch sawfly. Until it is known whether or not this is true, it is probably advisable to use estimates of foliage production only as a basis for comparing intensity of infestations in stands of different composition. If they are used to estimate the amount of food available, the data should be adjusted to compensate for the progressive increase in foliage weight.

2. The foliage sampling should be synchronized with the completion of linear foliage growth and be confined to as short a period as possible. Unless these two conditions are met the differences due to intra-seasonal weight increase may be as large as the inter-seasonal and inter-plot differences encountered.

3. The estimation of defoliation from samples taken before and after larval feeding must be supplemented by information on the percentage increase in foliage weight between the two sampling periods. Otherwise the amount of defoliation from sawfly attack will be seriously underestimated.

Summary

A technique is presented for estimating foliage production on tamarack. It provides bases for comparing the intensity of sawfly infestations in stands of different compositions, and for studying the effect of the insect upon its host.

Analyses of the data show that branches should be sampled from three crown levels per tree. Stratification of the trees on the basis of crown depth and crown form is recommended. Stratified samples of six branches from each of 30 trees should provide satisfactory estimates of amount of foliage per tree.

Foliage weight increases in a linear manner as the season progresses. The effects of this increase on a foliage sampling program are discussed.

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(Received April 28, 1959)

Termination of Diapause in the Douglas-Fir Beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera : Scolytidae), as an Aid to Continuous Laboratory Rearing[1]

By ROGER B. RYAN
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The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk., is a constant threat to Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests because of its ability to kill large quantities of this important timber tree. In the search for more effective control of this pest the need for experimental insects frequently exceeds the supply from natural sources. Laboratory rearing can alleviate this shortage.

Laboratory rearing of these bark beetles for experimental purposes offers the following advantages over collecting insects or beetle-infested logs in the field: (1) availability of insects throughout the year, (2) more generations per year than are obtainable under natural conditions, (3) increased brood survival, and (4) more homogeneous populations than occur in nature.

While rearing the Douglas-fir beetle at the Oregon State College Forest Insect Laboratory, one of the biggest problems encountered was that of terminating diapause in adults reared under a constant temperature. Emergence of adults from logs kept constantly at 75°F. was delayed and took place over a several month period. This paper describes experiments designed to evaluate the effects of low temperature treatments on the termination of diapause and subsequent emergence of laboratory-reared beetles.

Materials and Methods

Freshly emerged beetles were placed in cages containing three-foot lengths from recently cut Douglas-fir logs. Logs between eight and 15 inches in diameter were convenient. One or two days later, after the beetles had bored in, the logs were removed from the cages until the broods resulting from these attacks were ready to emerge. This procedure enabled more efficient space utilization during subsequent treatments. Prior to introducing the beetles, one end of each log was paraffin-coated to reduce evaporation. Moisture was supplied while the broods were developing by resting the untreated end of the log in moist sand. Ambient atmosphere was held at 75°F. and 60 per cent relative humidity. After intervals to be described later, the logs were transferred to walk-in coolers where the broods were subjected to a series of low temperatures for differing periods of time. After the cold treatments the logs were returned to the cages at 75°F. where emerging insects were collected daily for 30 days. At the end of this period each log was debarked and all remaining insects were counted.

The effectiveness of each cold rest treatment is expressed as the per cent of the insects emerging by the thirtieth day after the cold rest period ended. The rate of diapause termination of the beetles in each log, following the cold treatment, is expressed mathematically by the day of median emergence, or the day by which 50 per cent of the insects had emerged, and graphically by a curve of the cumulative per cent of emergence.

Experiments and Results

From 20 to 40 beetles were introduced into each of 45 logs. The logs were divided into three groups of 15 each. Each group was kept at 75°F. for one of

[1]Technical paper No 1204, Oregon Agricultural Experiment Station; part of a thesis submitted to Oregon State College, in partial fulfillment of the requirements for the M.S. degree. Financial support for this research has been provided by the Forest Protection and Conservation Committee of the Oregon State Board of Forestry, the Foundation for American Resource Management, and the Oregon Agricultural Experiment Station. The Northwest Forest Pest Action Council has been an active sponsor.

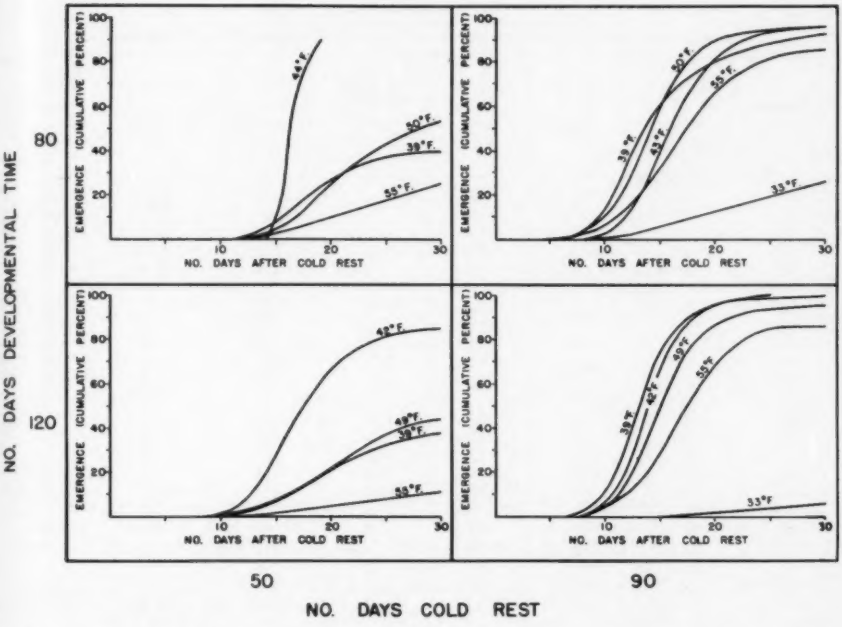

Fig. 1. Emergence of laboratory-reared beetles at 75°F. following various cold rest periods.

three periods, 40, 80, or 120 days, during which time the broods developed. Following these periods three logs from each group were placed at 33, 39, 43, 49, and 55°F. One log at each temperature from each group was left for 20, 50, and 90 days before being returned to 75°F. for observation of emergence. According to Vité and Rudinsky (1957) a 40-day period at 75°F. is just sufficient developmental time for the first eggs laid to reach the adult stage. They report also that the egg-laying period is two to three weeks. Therefore at the end of the 40-day developmental period in these experiments only a few insects had had time to reach the adult stage and most were in the late larval or pupal stage. This treatment is considered similar to conditions existing during the second beetle attack period under natural conditions where the adult stage is seldom reached before winter. After 80 days at 75°F. most of the brood were adults. The 80- and 120-day period were both used to ascertain whether the age of the adult beetles had an effect on their responsiveness to cold treatment.

Neither the 40-day developmental period in combination with any cold rest treatment nor any of the 20-day cold rest treatments was effective in terminating diapause, as only a few insects emerged during the 30-day emergence period following these treatments. For this reason these data have not been included in the tabular or graphical presentation of the results. Emergence data are presented in Fig. 1 and in Table I for the remaining treatments.

The relative effectiveness of the various cold treatments is graphically shown in Fig. 2. The divergences at the lower temperatures of the two 90-day cold rest curves and at the higher temperatures of the two 50-day curves were tested for significance by comparing logs 101 and 116, and 100 and 115 respectively, and

TABLE I

Summary of emergence from logs to which cold rest periods were applied[1]

Log. no.	No. days at 75°F. before cold rest	No. days cold rest	Temp. of cold rest °F.	No. brood emerged by 30th day after cold rest	Total no. brood and unemerged old adults	Percent emerged by 30th day	Day of median emergence
91	80	20	35	0	46	0	>30
92	80	20	39	0	188	0	>30
93	80	20	44	0	134	0	>30
94	80	20	50	0	39	0	>30
95	80	20	55	0	140	0	>30
96	80	50	35	0	18	0	>30
97	80	50	39	52	125	41.6	>30
98	80	50	44	9	10	90.0	16
99	80	50	50	357	672	53.1	28
100	80	50	55	147	571	25.7	>30
101	80	90	33	171	644	26.6	>30
102	80	90	39	374	403	92.8	13
103	80	90	43	547	567	96.5	16
104	80	90	49	535	558	95.9	14
105	80	90	55	362	426	85.0	17
106	120	20	33	0	162	0	>30
107	120	20	39	5	418	1.2	>30
108	120	20	42	5	394	1.3	>30
109	120	20	50	0	692	0	>30
110	120	20	55	3	747	0.4	>30
111	120	50	33	0	379	0	>30
112	120	50	39	44	115	38.3	>30
113	120	50	42	247	289	85.5	17
114	120	50	49	167	379	44.1	>30
115	120	50	55	32	267	12.0	>30
116	120	90	33	24	468	5.1	>30
117	120	90	39	470	472	99.6	13
118	120	90	42	350	352	99.4	14
119	120	90	49	162	169	95.9	15
120	120	90	55	46	55	83.6	17

[1]Not included are data for insects which had developed for 40 days at 75°F. and which had been subjected to cold rest, since emergence was negligible in all cases.

found to be significant at the .001 probability level by the normal deviate test (Li, 1957). The optimum temperature for diapause development was approximately 44°F.

Morphological and Physiological Manifestations of Diapause

Beetles which have emerged from the bark are physiologically mature. They are ready to attack other trees and establish broods, for they are capable of sustained flight and their gonads are fully mature (Vité and Rudinsky, 1957). In the present experiments beetles removed from the bark while in diapause made no attempts to fly. Dissection of these beetles showed that the flight muscles were extremely underdeveloped (Fig. 3). In addition, no eggs could be seen in the ovarioles of the females (Fig. 4), and the male seminal vesicles seemed underdeveloped when compared to those of mature individuals (Fig. 5). Probably the development of the flight muscles and the maturation of the gonads proceed concomitantly after some stimulus, in this case adequate chilling, has set in motion the proper endocrine activity (Lees, 1955).

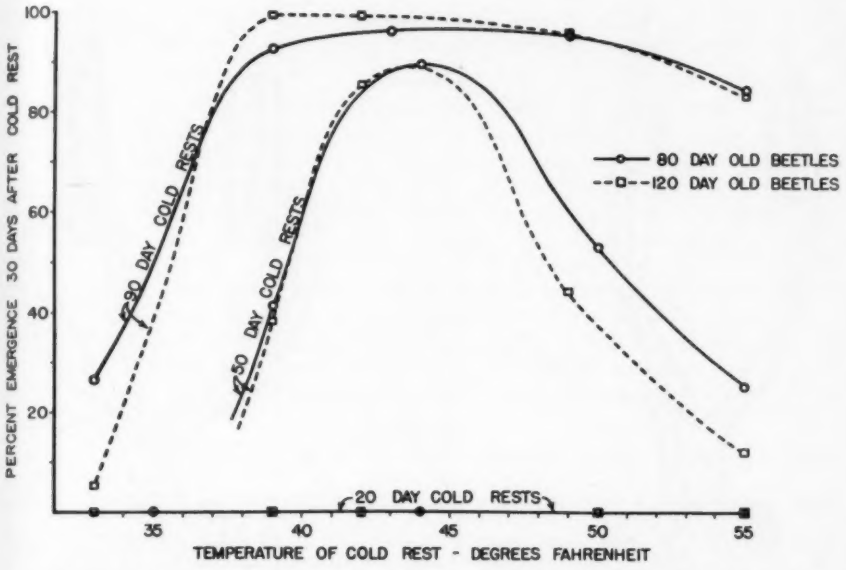

Fig. 2. Effectiveness of the various cold rest treatments as measured by the percent of emergence by the thirtieth day after treatment.

Discussion

To date, five laboratory generations have been reared using this method of exposure to low temperature. In the experiments described in this paper the minimum time to complete one generation was 146 days. This occurred in a log subjected to a 50-day cold treatment commencing 80 days after introducing the parents to the cage. The median emergence of the brood occurred on the sixteenth day following cold rest. However, these insects developed at an initial developmental temperature of 75°F. instead of at the optimum of 84-86°F. reported by Vité and Rudinsky (1957). According to these authors the brood reaches the adult stage approximately five days sooner at 84-86°F. than at

Fig. 3. Internal view of the right side of the thorax of two beetles showing the development of the main muscles of flight at two different times in the life cycle. Left: beetle in diapause. Right: mature beetle.

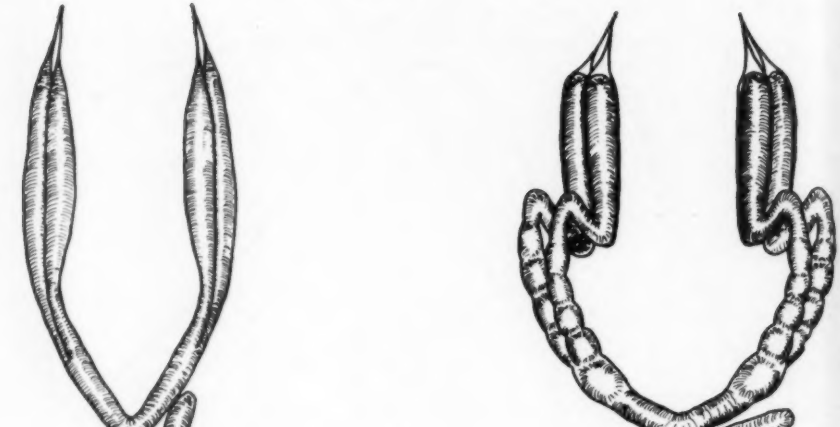

Fig. 4. Ovaries of two females showing the development at two different times in the life cycle. Left: beetle in diapause. Right: mature beetle.

73-75°F. It may reasonably be assumed, therefore, that the cold treatment may be applied five days sooner or when the beetles have developed at 84 to 86°F. for 75 days. The total elapsed time then would be 141 days for a complete generation, a rate of 2.6 laboratory generations per year. It should be pointed out that the minimum developmental time at 75°F. and the minimum duration of the cold rest have been ascertained only to lie between the wide limits of 40 and 80, and 20 and 50 days, respectively. Therefore, with further experiments the 141 days necessary for one generation probably could be reduced still further to bring the

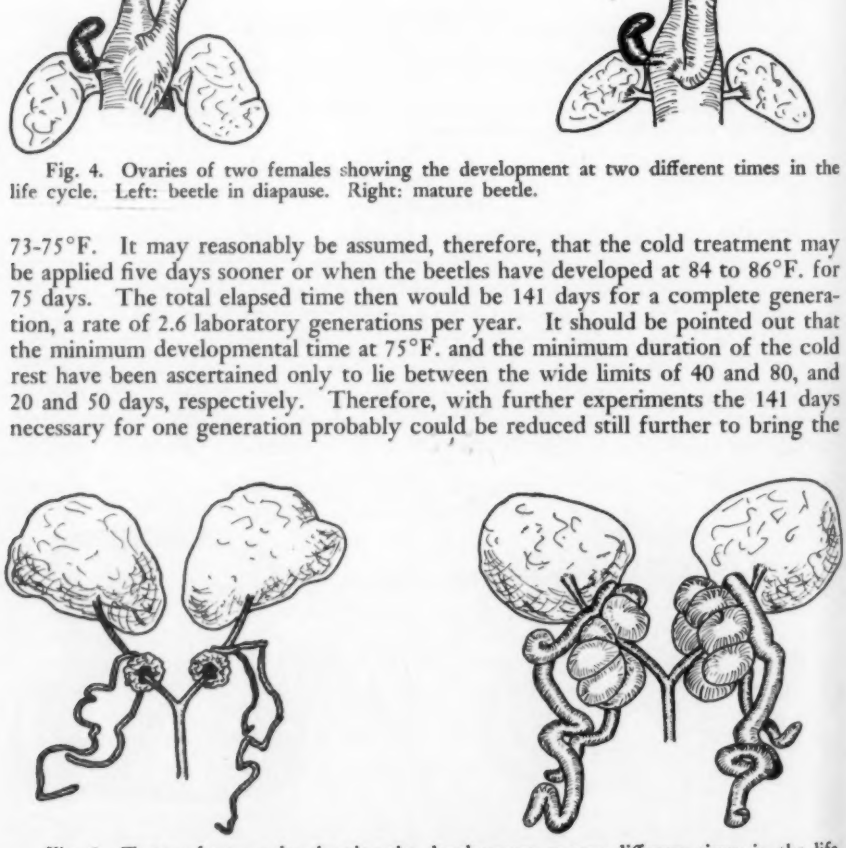

Fig. 5. Testes of two males showing the development at two different times in the life cycle. Left: beetle in diapause. Right: mature beetle.

total number of generations possible per year closer to three. This represents a marked increase over the one generation per year under natural conditions.

Summary

Freshly emerged Douglas-fir beetles were allowed to attack three-foot sections of recently cut Douglas-fir logs. After developing at 75°F. in the logs for differing periods, the broods of these insects were subjected to various low temperatures for differing periods. Following cold treatment the logs were caged at 75°F. and emerging insects were collected daily for 30 days. All logs were then debarked and remaining insects counted. The optimum temperature for diapause development was approximately 44°F. The minimum developmental period at 75°F. and the minimum duration of cold rest which were effective in terminating diapause lay between 40 and 80, and 20 and 50 days, respectively. Ninety-day cold treatments were more effective than 50-day treatments. Adult beetles in diapause have underdeveloped flight muscles and gonads. Several generations per year can be reared in the laboratory by applying the procedures described.

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(Received February 9, 1959)

Note on Occurrence of the Fungus *Empusa muscae* Cohn on Adults of the Onion Maggot, *Hylemya antiqua* (Meig.) (Diptera: Anthomyiidae)[1]

By L. A. Miller and R. J. McClanahan
Entomology Laboratory, Chatham, Ontario

During studies on the control of the onion maggot, *Hylemya antiqua* (Meig.), in late September, 1958, from one to 10 dead adults were found clinging to the tops of onion leaves in a three-acre field of green bunching onions in the Toronto area (Fig. 1). The dead flies were more abundant in the outside three rows, adjoining a non-cultivated grassy area, than throughout the rest of the field. A fungal growth was evident between the abdominal terga and sterna in many specimens. Infected live flies were somewhat pale, appeared bloated, and moved very sluggishly in comparison with non-infected adults. Dead flies were sent to Dr. G. Bucher, Entomology Laboratory, Belleville, Ontario, who identified the pathogen as *Empusa muscae* Cohn.

There are many records in entomological literature of *E. muscae* infections (Steinhaus, 1949). The fungus is most common on species of Muscidae, Calliphoridae, Scatophagidae, and Syrphidae but its occurrence in the Anthomyiidae seems quite rare. In England, Gough (1947) reported that adults of the lesser bulb fly, *Leptohylemyia coarctata* Fall. (Anthomyiidae), are sometimes attacked by a fungus of the "*Empusa* type" but that not many flies are killed by the organism even in wet seasons. Chittenden (1902) recorded *E. americana* infecting adults of the seed-corn maggot, *Hylemya cilicrura* (Rond.), in Alabama. This is the first report of the fungus on onion maggot adults in Canada and re-

[1]Contribution No. 3924, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

Fig. 1. Onion maggot adults infected with the fungus *Empusa muscae* Cohn.

searchers in the states of Washington, Wisconsin, Michigan, and New York have not observed similar infections in these areas (personal discussions).

The symptomology of *E. muscae* on *H. antiqua* adults is very similar to that of *E. grylli* (Fres.) on grasshoppers as reported by Skaife (1925).

The literature indicates that *Empusa* spp., including *E. muscae*, more commonly become epizootic during periods of high humidity and cool weather towards the end of summer (Dresner, 1949; Roubaud, 1922). Such weather prevailed in the Toronto area for about one week before the disease was observed. Steinhaus (1954) and many others have discussed the positive relationship between the population density of the host and the incidence of disease. An unprecedented outbreak of the onion maggot in almost all onion-growing areas of southern Ontario was an outstanding feature of the 1958 vegetable-growing season. Adults were present in outbreak numbers from mid-June until late October. The populations were so large that infestations of this highly host-specific insect were found in radish and spinach planted where maggot-infested onions had been disked under.

This outbreak of *E. muscae* was, therefore, probably associated with the period of high humidity and cool weather in the season but, perhaps more significantly, with the unusually high population density. Local factors must also have been operative, as it is noteworthy that, although numerous fields were periodically examined, the disease was observed in only the one mentioned.

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(Received March 17, 1959)

Note on Fecundity of the Pea Aphid, *Acyrthosiphon pisum* (Harris), Caged on Plants of Broad Bean, *Vicia faba* L., Treated with Various Plant Growth Regulators

By A. G. Robinson

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The effect on insect populations of the widespread use of plant growth regulators and herbicides is a neglected field. Fox (1948) reported on a relationship between the use of 2,4-D and wireworm damage to wheat. Putnam (1949) suggested that 2,4-D could be an environmental factor in the ecology of grasshoppers. A recent report (Maxwell and Harwood, 1958) indicates that even slight dosages of 2,4-D increase the rate of reproduction of pea aphids on broad beans. This note is a preliminary report on similar investigations with the pea aphid, *Acyrthosiphon pisum* (Harris), and broad bean, *Vicia faba* L.

Four chemical compounds have been tested: MH (maleic hydrazide 40 per cent soluble powder), 2,4-D (2,4-dichlorophenoxyacetic acid 50 per cent amine), 2,4,5-T (2,4,5-trichlorophenoxyacetic acid 42.5 per cent ester) and MCPA (2-methyl-4-chlorophenoxyacetic acid 50 per cent amine). Prior to the actual tests on insects, dosages were established whereby broad bean showed injury but not plant mortality.

Plants of Windsor broad bean were grown in soil to a height of one to three inches and then transplanted into vermiculite (Zonolite) in individual 3½-inch clay pots. Solutions of plant growth regulators were added to the vermiculite in the pots, and root absorption of the chemical was allowed to continue for 48 hours. For each chemical used, one set of plants was treated with tap water as a control. A nutrient solution of Plant Prod 20-20-20 sustained the plants for the remainder of the test.

Ninety-six hours after the plant had been first treated with the plant growth regulator, one of the lower double leaves of the plant was removed, to facilitate enclosing the remaining leaf in a cage of Visking dialyzing tubing (36 mm. diameter). One female pea aphid (apterous summer vivipara) was placed on the leaf in the cage. Adults placed in the cages were 12 to 15 days old. They remained in the cages for five days, at which time counts were made on mortality and fecundity. Greenhouse temperatures varied between extremes of 50 to 100°F, but averaged about 70°F. Relative humidity varied between extremes of 40 to 100 per cent, but averaged about 70 per cent. Lights above the plants were turned off between midnight and 8 A.M.

Results shown in Table I indicate that maleic hydrazide by root absorption caused both nymphal mortality and reduced fecundity at rates of 4,000, 3,000 and 2,000 p.p.m. Nymphs were rarely observed beyond the first instar, and many of them were born dead. The results confirmed a previous test on July 5 in which essentially the same results were obtained.

Root absorption of 2,4-D by broad bean at rates of 2,1, 0.5, 0.1 and 0.01 p.p.m. had no effect on adult or nymphal mortality, or adult fecundity. Similarly 2,4,5-T at rates of 0.1, 0.01, 0.001 and 0.0001 p.p.m. had no effect on adult or nymphal mortality, or adult fecundity. MCPA at rates of eight, four, two, one, and 0.1 p.p.m. had no effect on adult or nymphal mortality, or adult fecundity. In all cases there was no significance between transformed averages of fecundity, and the checks.

TABLE I

Adult and nymphal survival, and fecundity, of the pea aphid after five days caged on broad beans treated August 7, 1958, with maleic hydrazide

Rate of application p.p.m.	No. of live adults	No. of dead adults	Total progeny	Total No. of dead nymphs	Average No. of live progeny of live adults	Transformed Average[1]	Range
4000	8	12	71	66	0.6	0.98**	0–3
3000	17	3	173	125	2.5	1.45**	0–16
2000	16	4	171	119	3.2	1.74**	0–12
Water only	20	0	336	0	16.8	4.04	5–37

[1]Mean transformed by using $\sqrt{x + 0.5}$
**Significant at the 1% level.

Harwood (in litt.) has stated that the method used by Maxwell and Harwood (1958) to apply 2,4-D was by dipping the lower double leaf of broad bean in a solution. This appears to be a more appropriate technique than that of root absorption reported in this note, because it corresponds more closely to the practical application of a herbicide in the field.

This investigation will be continued, adopting the leaf-dipping technique, with a series of various plant growth regulators or herbicides. Chromatographic analyses of the leaves will be made with a view to associating changes in plant chemistry with the effects on the aphids.

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(Received February 19, 1959)

Results of the Recent Election

The Election Committee has reported that of the 478 ballots mailed to the members entitled to vote, 309 were returned, with the following members elected.

President elect, 1959-60	Dr. A. P. Arnason
Directors at large, 1959-61	Mr. J. G. Rempel; Mr. J. A. Downes; Dr. B. M. McGugan.
Directors representing regional entomological societies, 1959-61	Dr. L. Daviault, Quebec; Mr. P. H. Westdal, Manitoba; nominee to be selected, Alberta.

L. L. Reed, *Secretary*.

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